Habitat Requirements and Life History Characteristics of Selected Marine Invertebrate Species Occurring in the Newfoundland and Labrador Region

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by

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ABSTRACT

Knowledge of the habitat utilized by various invertebrate species and their different life stages is necessary to effectively manage fish and fish habitat, particularly when assessing the potential impacts of various project developments. This habitat requirements document was developed as a tool to assist proponents and habitat managers in quantifying any harmful alteration, disruption, or destruction (HADD) of fish habitat resulting from various project developments. It will allow all marine habitats upon which various species depend in order to carry out their life processes to be taken into consideration during project reviews and subsequent decision-making. It is also intended to serve as a resource for proponents in developing project referrals as well as streamline/expedite the review of these referrals by habitat managers, resulting in client needs being met in a timely and efficient manner.

An extensive literature review was performed to compile information on habitat use among various life stages of selected invertebrate marine species occurring throughout Newfoundland and Labrador. Vertical habitat zone, horizontal habitat zone, exposure, salinity, currents, water temperature, substrate type and aquatic vegetation were the main physical habitat features considered. Overall, there is a general lack of certainty pertaining to the marine habitat requirements for many invertebrate species in Newfoundland and Labrador. Within the marine environment, there are often seasonal and temporal shifts in habitat use, differences related to early life history requirements, food availability, spawning requirements and the likelihood of overwintering survival, plus the effects of intra- and inter-specific competition, predation and various environmental variables. All these factors may cause shifts in habitat utilization.

This report describes the habitat of various animals that represent some of the Phyla that classify marine invertebrate animals. These Phyla include Cnidaria, Ctenophora, Mollusca, Annelida, Arthropoda, Echinodermata and Bryozoa. Forty-three species plus eleven genera are discussed in the report with respect to their various habitat requirements. While the species list presented is certainly not a comprehensive one, it is one that was chosen to be representative of those significant in the commercial fishery or that play a role in the production of the commercial fishery. As the knowledge base of marine invertebrates is continuing to slowly grow, it is intended that there will be future updates that include new information, taxonomic revision as well as an expanded species list.

RÉSUMÉ

Il est nécessaire de connaître l'habitat utilisé par diverses espèces d'invertébrés et les différentes étapes de leur cycle biologique pour gérer efficacement le poisson et l'habitat du poisson, particulièrement lorsqu'il s'agit d'évaluer les impacts potentiels de divers projets d'aménagement. Ce document sur les besoins en matière d'habitat a été élaboré pour aider les promoteurs et les gestionnaires de l'habitat à mesurer la détérioration, la destruction ou la perturbation (DDP) de l'habitat du poisson découlant de divers projets d'aménagement. Il permettra de tenir compte de tous les habitats marins dont dépend le processus vital de nombreuses espèces lors de l'examen des projets et dans les décisions qui en découlent. Il pourrait aussi être utile aux promoteurs pour la recommandation de projets, et permettre de rationaliser/d'accélérer l'étude des recommandations par les gestionnaires de l'habitat et, partant, de répondre efficacement et en temps voulu aux besoins des clients.

On a consulté et étudié de nombreux documents scientifiques pour regrouper des données sur l'utilisation de l'habitat par certaines espèces d'invertébrés marins présentes à Terre Neuve et au Labrador, à divers stades de leur cycle biologique. Les principales caractéristiques physiques de l'habitat qui ont été étudiées sont la zone d'habitat vertical, la zone d'habitat horizontal, le degré d'exposition, la salinité, les courants, la température de l'eau, le type de substrat et la végétation/flore. Globalement, on note de grandes incertitudes quant aux besoins en matière d'habitat marin de nombreuses espèces d'invertébrés présentes à Terre Neuve et au Labrador. Dans le milieu marin, on note de fréquentes variations, tant spatiales que temporelles, dans l'utilisation de l'habitat. Ces variations sont imputables à divers facteurs dont les besoins durant les premiers stades du cycle biologique, la disponibilité de la nourriture, les besoins en matière de reproduction ou la probabilité de survie à l'hiver, mais également les effets de la concurrence et de la prédation intraspécifiques et interspécifiques, et d'autres variables environnementales.

Ce rapport décrit l'habitat de divers animaux représentatifs de certains embranchements d'invertébrés marins, au nombre desquels les cnidaires, les cténophores, les mollusques, les annélides, les arthropodes, les échinodermes et les bryozoaires. Le rapport porte sur les divers besoins en matière d'habitat de quarante trois espèces et onze genres. Bien que non exhaustive, la liste présentée a été choisie parce qu'elle comprend des espèces importantes dans la pêche commerciale ou qui jouent un rôle dans la production de la pêche commerciale. Au fur et à mesure que la base de connaissances sur les invertébrés s'élargira, on mettra cette liste à jour, notamment en y ajoutant de nouvelles données et d'autres espèces, et en effectuant des révisions taxonomiques.

1.0 INTRODUCTION

DFO is responsible for the conservation and protection of fish habitat in Newfoundland and Labrador (NL), which is accomplished in part through administering the habitat protection provisions of the *Fisheries Act*. Subsection 35(1) of the *Fisheries Act* prohibits the harmful alteration, disruption or destruction (HADD) of fish habitat unless authorized by the Minister. In recent years, both habitat managers and proponents have realized that a repeatable and scientifically defensible method is necessary to assist with the implementation of the *No Net Loss* guiding principle of DFO's *Policy for the Management of Fish Habitat* when assessing potential impacts to fish habitat within the marine environment. Under this *Policy*, DFO strives to balance unavoidable habitat losses with habitat replacement so that Canada's fisheries resources are not impacted.

The majority of all described species of animals are invertebrates. Within the vast array of invertebrate animals, there is a wide range in size, structural diversity and adaptations to different modes of existence. Understanding the diversity and complexity of habitat use by various invertebrate species and their life stages is an important step for the effective management of fish habitat. This knowledge is particularly important when assessing potential impacts on fish habitat resulting from various development activities such as oil and gas exploration and development, aquaculture operations, and the construction of various types of marine infrastructure including; wharves, causeways, marinas, breakwaters, slipways, trans-shipment terminals, etc. Having this habitat information available ensures that all marine habitats upon which invertebrate species depend in order to carry out their life processes, are taken into consideration during project reviews and subsequent decision-making. It will also assist proponents in developing project referrals as well as expedite the review of these referrals by habitat managers, resulting in client needs being met in a timely and efficient manner.

An extensive literature review was performed to compile information on marine habitat requirements/preferences of various life stages (spawning, fertilized eggs, larvae, immediate post-larva, juveniles and adults) of invertebrate species occurring throughout Newfoundland and Labrador. This report describes the habitat of various animals which represent some of the Phyla that classify marine invertebrate animals. These Phyla include Cnidaria, Ctenophora, Mollusca, Annelida, Arthropoda, Echinodermata and Bryozoa. Forty-three species plus eleven genera are discussed with respect to their various habitat requirements (Table 1). The general aspects researched, as they pertain to habitat requirements, include broad and fine scale distributions, life cycle stages and predator-prey relationships. All species/groups discussed occur in Newfoundland and Labrador waters, although some are more abundant in other parts of Atlantic Canada. The list of species is certainly not complete. Some were chosen because of their significance in commercial fisheries, while others, although not harvested commercially, play important roles in the production of commercial invertebrate and vertebrate species. As the knowledge base of marine invertebrates continues to grow, it is intended that there will be future updates to this document, including new information, any taxonomic revision, as well an expanded species list.

Table 1. A list of the forty-three species and eleven genera included in the literature review.

	Genus/Species	Group	Phylum
1.	*Obelia* spp.	Hydrozoan	Cnidaria
2.	*Dynamena* spp.	Hydrozoan	Cnidaria
3.	*Clava multicornis*	Hydrozoan	Cnidaria
4.	*Cyanea capillata*	Scyphozoan	Cnidaria
5.	*Aurelia aurita*	Scyphozoan	Cnidaria
6.	*Metridium senile*	Anthozoan	Cnidaria
7.	*Urticina feline*	Anthozoan	Cnidaria
8.	*Pleurobrachia pileus*	Comb Jelly	Ctenophora
9.	*Bolinopsis infundibulum*	Comb Jelly	Ctenophora
10.	*Littorina littorea*	Gastropod	Mollusca
11.	*Littorina obtusata*	Gastropod	Mollusca
12.	*Buccinum undatum*	Gastropod	Mollusca
13.	*Ensis directus*	Bivalve	Mollusca
14.	*Arctica islandica*	Bivalve	Mollusca
15.	*Spisula solidissima*	Bivalve	Mollusca
16.	*Mactromeris polynyma*	Bivalve	Mollusca
17.	*Mya arenaria*	Bivalve	Mollusca
18.	*Serripes groenlandicus*	Bivalve	Mollusca
19.	*Clinocardium ciliatum*	Bivalve	Mollusca
20.	*Modiolus modiolus*	Bivalve	Mollusca
21.	*Mytilus edulis*	Bivalve	Mollusca
22.	*Chlamys islandica*	Bivalve	Mollusca
23.	*Placopecten magellanicus*	Bivalve	Mollusca
24.	*Illex illecebrosus*	Cephalopod	Mollusca
25.	*Loligo pealeii*	Cephalopod	Mollusca
26.	*Gonatus fabricii*	Cephalopod	Mollusca
27.	*Bathypolypus arcticus*	Cephalopod	Mollusca
28.	*Nereis* spp.	Polychaete	Annelida
29.	*Arenicola marina*	Polychaete	Annelida
30.	*Amphitrite* spp.	Polychaete	Annelida
31.	*Spirorbis* spp.	Polychaete	Annelida
32.	*Nephtys* spp.	Polychaete	Annelida
33.	*Myxicola infundibulum*	Polychaete	Annelida
34.	*Homarus americanus*	Decapod	Arthropoda
35.	*Pandalus borealis*	Decapod	Arthropoda
36.	*Crangon septemspinosa*	Decapod	Arthropoda
37.	*Chionoecetes opilio*	Decapod	Arthropoda
38.	*Cancer irroratus*	Decapod	Arthropoda
39.	*Hyas araneus*	Decapod	Arthropoda
40.	*Hyas coarctatus*	Decapod	Arthropoda
41.	*Pagurus* spp.	Decapod	Arthropoda
42.	*Meganyctiphanes norvegica*	Euphausiid	Arthropoda

	Genus/Species	Group	Phylum
43.	*Thysanoessa* spp.	Euphausiid	Arthropoda
44.	*Strongylocentrotus droebachiensis*	Echinoid	Echinodermata
45.	*Cucumaria frondosa*	Holothuroid	Echinodermata
46.	*Ophiopholis aculeata*	Ophiuroid	Echinodermata
47.	*Amphipholis squamata*	Ophiuroid	Echinodermata
48.	*Ophiura* spp.	Ophiuroid	Echinodermata
49.	*Asterias rubens*	Asteroid	Echinodermata
50.	*Leptasterias polaris*	Asteroid	Echinodermata
51.	*Solaster endeca*	Asteroid	Echinodermata
52.	*Echinarachnius parma*	Echinoid	Echinodermata
53.	*Membranipora* spp.	Bryozoan	Bryozoa
54.	*Alcyonidium* spp.	Bryozoan	Bryozoa

2.0 METHODS

An extensive literature search was carried out to obtain information on marine habitat utilization of the different life stages of various invertebrate species occurring within the Newfoundland and Labrador Region. Emphasis was placed on information sources and habitat requirements specific to the region. Information was derived from as many sources as possible, including primary literature, grey literature (i.e., government reports, consultant reports), academic texts and the internet. The information sources used include:

- DFO Species Profile Series;
- DFO Underwater World Factsheets;
- Scientific reports;
- DFO publications, including Technical, Manuscript and Stock Status Reports;
- Research theses;
- Fisheries and Aquatic Sciences Abstracts;
- Consultation with regulatory authorities (regional, national and international) and academic communities.

For marine invertebrate species, six life stages were identified: i) spawning – individuals in spawning condition, ii) fertilized eggs, iii) larvae - individuals under one year of age (0+), iv) immediate post-larvae, v) juveniles - individuals older than one year of age, but not sexually mature and vi) adults - individuals that have reached sexual maturity, but are not in spawning condition.

The habitat requirements associated with each of the life cycle stages were described based on the following biophysical habitat features; i) vertical habitat zone (as per Table 2), ii) horizontal habitat zone (as per Table 3), iii) substrate (as per Table 4); iv) degree of exposure, v) tide/currents, vi) water temperature, vii) salinity and viii) aquatic vegetation.

Table 2. Characterization of vertical habitat zone.

Vertical Habitat Zone	Definition
Pelagic	Open ocean waters, either middle or surface water levels, which are not directly influenced by the shore or bottom.
Demersal	Living on, at or near the bottom of the ocean.
Benthic	Living on the bottom of the ocean.
Infauna	Living in the substrate, especially in a soft sea bottom.

Table 3. Characterization of horizontal habitat zone.

Horizontal Habitat Zone	Definition
Splash	All land above high tide area.
Intertidal	Includes the area between high and low water marks.
Shallow Subtidal	The shallow water zone from the extreme low tide level to a depth of around 30 m.
Deep Subtidal	The water zone extending from 30 m to a depth of approximately 200 m.

Substrate

Substrate type was classified according to particle size as a derivation of the Wentworth-Udden particle scale (Wentworth 1922) as illustrated in Table 4.

Table 4. Characterization of various substrates into classes by particle size.

Substrate Type	Definition
Bedrock	Continuous solid bedrock
Boulder	Rocks greater than 250 mm in diameter
Cobble	Rocks ranging from 30 - 250 mm
Gravel	Rocks ranging from 2 - 30 mm
Sand	Fine deposits ranging from 0.06 - 2 mm
Mud (silt and clay)	Material encompassing both silt and clay; < 0.06 mm
Organic/Detritus	A soft material containing 85% or more organic materials such as decayed aquatic plants and animals
Shells	Calcareous remains of shellfish or invertebrates containing shells

3.0 RESULTS

3.1 CNIDARIA

3.1.1 Hydroids (*Obelia* spp.; *Dynamena* spp.; *Clava multicornis*)

General Information

Hydrozoa is a class of animals within the Phylum Cnidaria, hydroids being the dominant polyp stage of the hydrozoans (Gosner 1979). The oral end of the polyp bearing the mouth and tentacles is known as the hydranth and the stalk of the polyp is referred to as the hydrocaulus. In most species of hydrozoans, the colony is anchored to the substrate by the hydrorhiza from which polyps arise. All hydroid colonies are dimorphic in that the colony consists of at least two structurally and functionally different types of individuals; 1) feeding polyps known as gastrozooids and 2) sexually reproductive individuals known as medusoids. The gastrozooids capture and ingest zooplankton small enough to be handled by the tentacles. The medusoids either develop into free medusae (e.g., *Obelia* spp.) or are retained on the colony as sexual buds known as gonophores (e.g., *Dynamena* spp., *Clava multicornis*). The majority of hydroids retain their medusoid stages as sessile gonophores in which the gametes develop (Barnes 1980).

Although hydroids rarely settle on shallow soft bottoms, they inhabit softer substrates at greater depths (Boero 1984). Shumway *et al.* (2003) demonstrated the detrimental and potentially lethal impacts of suspended clay particles on sedentary, benthic organisms, including hydroids that rely on filtration during feeding. Boero (1984) discussed several habitat factors that contribute to the determination of spatial and temporal distributions of hydroids; water movement, light, salinity, air exposure, food availability, pollution and water temperature. Sagasti *et al.* (2000) examined the abundance and species composition of sessile and mobile epifaunal assemblages in a U.S. estuary with hypoxic episodes. They found that hydroids were equally abundant in the areas with different oxygen levels.

Hydroids and bivalves often form highly reciprocal commensal relationships. Juvenile bivalves use hydroids for spat attachment and protection from predators (Pulfrich 1996). The hydroids continue to provide camouflage and protection from predators, parasites and injuries as the bivalves grow. In return, bivalves provide hydroids with space for settlement and subsequent access to water currents, nutrition and spatial refuges from predators. Thus, hydroids may prefer to settle on bivalve hosts rather than on inert substrate particles (Henry and Kenchington 2004).

Calder (1990) investigated the seasonal cycles, activity and inactivity of some hydroid species found in estuaries from Virginia and South Carolina. Of the species considered, four had reported northern range limits that included Newfoundland and Labrador. The minimum-maximum activity temperature range for each of these four species was 3 to 25 °C.

Information Specific to *Obelia* spp., *Dynamena* spp. and *Clava multicornis*

Obelia spp.: *Obelia* species exhibit both the polypoid and hydromedusoid stages, the latter being planktonic (Gosner 1979; Stepanjants 1998). Barnes (1980) concisely described the general life cycle of *Obelia* spp. The hydromedusae are generally dioecious. Fertilization may occur externally in the seawater, on the surface of the medusae, or internally in the gonad. The

fertilized eggs develop into relatively short-lived, lecithotrophic planula, ovoid free-swimming ciliated larvae typical of cnidarians. The planulae may remain free-swimming from several hours to several days after which they attach to substrates and develop into a hydroid colony.

Hooper (1997) identified these epiphytic hydroids (in this case, living attached to kelp) as key animals of the biota assemblage associated with the "kelp bed" habitat that he described as one of numerous marine coastal habitat types found in Newfoundland and Labrador. Typical physical characteristics attributed to this habitat type include hard substrates (bedrock/boulder), high salinity, lower water temperatures, reduced ice scour and moderate to high exposure to wave energy (Hooper 1997).

In Bonne Bay, Newfoundland, Penton (2003) encountered two species of *Obelia*, *Obelia geniculata* and *Obelia longissima*. These two hydroid species are often used as nursery areas for juvenile nudibranchs. *O. geniculata* was found growing on various kelp species (*Laminaria* spp. and *Agarum crobrosum*), while *O. longissima* was growing on bedrock.

Henry and Kenchington (2004) described differences between epilithic and epizoic hydroid assemblages from commercial scallop grounds in the Bay of Fundy. While the number of hydroid taxa was significantly lower on cobble than on scallops, Henry and Kenchington (2004) concluded that the predominance of *Obelia dichotoma* on scallops does not necessarily reflect an affinity for scallop hosts over cobbles. The authors pointed out that *O. dichotoma* exhibits a wide tolerance of substrate host-type and has been found attached to both inert and living substrates, both sessile and mobile, including shark fins, turtles, sea horses and crustaceans (Cornelius 1995). *O. geniculata* and *O. longissima* were also identified from samples taken at the Bay of Fundy scallop grounds.

Sullivan *et al.* (1997a) reported floating colonies of hydroids, made up primarily of *Clytia gracilis*, on Georges Bank in May. *Obelia* and *Clytia* species often co-occur as evidenced by zooplankton sampling (Madin *et al.* 1996). Sullivan *et al.* (1997a) found the highest densities of *C. gracilis* inshore of the 40 to 60 m isobaths in cold, well mixed water where the shelf-slope front intersected the bottom and tidally induced turbulence resulted in strong vertical mixing. Divers observed actively feeding hydroid colonies in the upper 10 m of the water column, suspended by the turbulent mixing in the bottom boundary layer caused by strong tidal flows. These planktonic occurrences were surprising given that polyps of hydrozoans are normally found attached to seaweed, rocks or shells, or feeding on organisms in the benthic region. Hydroids had been reported in Georges Bank plankton prior to this study (Fraser 1915). Hydrozoan polyps were virtually absent in the offshore, deepwater (60 to 100 m) plankton.

During a two-year study in the St. Lawrence Estuary, Brault and Bourget (1985) observed that *O. longissima* was one of the early colonizers on artificial substrates and eventually dominated and determined the community structure. Their study area was a boulder field in 5 m of water where temperature and salinity ranged from –1 °C (January) to 12.5 °C (August) and 25.5 to 31.5 ppt, respectively. Bourget *et al.* (2003) described the distribution of epibenthic invertebrate biomass on suspended collectors (navigation buoys) in the St. Lawrence system in relation to environmental factors over a nine-year period. The environmental data included surface water temperature, water salinity, water transparency, current velocity, chlorophyll *a* and primary

production. Water temperature, water transparency, biogeographic groups of buoys and primary production explained approximately 70% of the variability in *O. longissima* biomass distribution.

Hydroids occurring in patches are likely to be important competitors (feed on similar sized zooplankton) and predators of larval fish considering the highly overlapping vertical and horizontal distributions of hydroids and fish larvae reported during studies conducted on Georges Bank (Madin *et al.* 1996; Sullivan *et al.* 1997a). Madin *et al.* (1996) found indications that hydroids were capable of consuming from 50 to 100% of the daily production of young copepods, prey also utilized by larvae of fish including cod and haddock. *C. gracilis* was the predominant hydroid found by Madin *et al.* (1996), although *Obelia* sp. was also present in the samples. Laboratory experimentation has also indicated the capability of hydroids to consume larval fish, even though the larvae were much larger than the hydranths (Fraser 1915; Madin *et al.* 1996). Klein-MacPhee *et al.* (1997) also concluded that cod and haddock larvae (6 to 10 mm length) were small enough to be subject to predation by hydroids.

Hydroids may represent an important link between trophic levels. Avent *et al.* (2001) studied the potential role of predation by fish upon unattached hydroids on Georges Bank, principally *C. gracilis*. Hydroids were rarely found to be an important part of the diets of the wide variety of fish that had hydroids in their stomachs. The most important predator of these cnidarians on the Georges Bank was Winter Flounder. Fish off the coast of North Carolina have also been documented as predators of hydroids (Stachowicz and Lindquist 1997).

Calder (1990) investigated numerous hydroid species occurring in estuaries of Virginia and South Carolina. Observed ranges of water temperature within which activity was evident in two species of *Obelia* were 10 to 32 °C and 8 to 30 °C. He further separated "cold water" species from "warm water" species on the list of hydroids studied. He concluded that the optimal activity temperature range for the "cold water" species was 3 to 25 °C. Calder (1990) concluded that the abrupt and predictable appearances of hydroids at particular water temperatures and seasons suggested the existence of "resting stages" that were tolerant of unfavourable seasonal environmental extremes.

Pagès *et al.* (1996) studied the diets of gelatinous zooplankton off Norway during spring 1992. The medusae of *Obelia* spp. were among the most abundant biota (up to 158 individuals m^3) in the upper 50 m of the water column where a strong halocline (28.2 to 34.5 ppt) was present. The main prey items found in the medusae were various copepods.

The natural diet of the epiphytic hydrozoan *O. geniculata* was studied in an upwelling area in the Bay of Coliumo in Chile (Orejas *et al.* 2000). Orejas *et al.* (2000) found that during two 24-hour cycles, more than 78% of the diet consisted of invertebrate eggs and faecal pellets and that capture rate was hardly related to the peaks of prey abundance. The mean ingestion rate observed was about 113% of the hydranth (nutritive zooid in a hydrozoan colony) biomass per day. The authors concluded that their results indicated the importance of small sized benthic suspension feeders in upwelling systems.

Dynamena spp. (aka *Sertularia*) (Garland hydroids) and *Clava multicornis* (Club Hydroid): Particular species of *Dynamena* occur in the northwest Atlantic Ocean from the Arctic to Cape

Hatteras. They are common on seaweeds, rocks and pilings from the lower intertidal zone to considerable depths in the subtidal zone. *Dynamena* species do not have the hydromedusa stage (free medusae) in their life histories (Gosner 1979).

The distribution of the Club Hydroid, *C. multicornis*, in the northwest Atlantic Ocean is from Labrador to Long Island Sound in the intertidal and shallow subtidal zones (Gosner 1979). *C. multicornis* typically occurs in clumps or patches on rockweeds and knotted wracks.

The general life cycle pertaining to *Dynamena* spp. and *C. multicornis* is described in Barnes (1980). Rather than being free-swimming, the medusae in these species remain attached to the parent hydroid and degenerate, yet are capable of reproduction. The Club Hydroid has its gonophores in berrylike clusters on the hydranth region. Larvae develop from fertilized eggs and eventually attach to the substrate to begin a new hydroid colony.

In the asexual reproduction of *C. multicornis*, the gonophores develop in dense, bud-like clusters just below the tentacles. The gonophores are very degenerate in both sexes, retaining few traces of the medusa structure. Only a few eggs are present in each of the female gonophores. With respect to the sexual reproduction of *C. multicornis*, fertilization is internal and the oval-shaped embryo elongates, becomes ciliated and acquires the beginning of the coelenteron. At this stage, the planulae burst from the gonophores. The free-swimming planula creeps about for some time and eventually becomes fixed at its broad anterior end. It then loses its cilia, flattens out and elongates in the direction of the main body axis. The first tentacles then appear at the free end, resulting in a functional hydroid (Costello 1971).

Orlov (1996) described larval settlement by *Dynamena pumila*, a common hydroid in northern and temperate seas. This species typically lives on brown algae (e.g., *Laminaria* sp., *Fucus* sp.) in areas with moderate to high exposure to waves and currents. The crawling planulae of *D. pumila* appeared far more resistant to rapid water flows than the planulae of other hydroids. Seed and O'Connor (1981) described the association between *D. pumila* and *Fucus serratus* at a sheltered location with bedrock, stones and small boulders in Wales. *D. pumila* was found throughout the entire intertidal zone at a sheltered rocky location in the North Sea (Janke 1986).

Henry (2002) assessed the vertical zonation and temporal dynamics of *D. pumila* across a wave-exposure gradient on five rocky shores in the Bay of Fundy. Abundance peaked at about 37.5-62.5% of the mean tidal range, with maximum abundance at moderate wave exposure. Abundance peaked during the summer and dropped dramatically during the winter, especially at the more wave exposed locations. Henry (2002) demonstrated the dramatic shifts in the distribution, fertility and size of *D. pumila* and highlighted the importance of wave action, ice scour and seasonal changes in environmental conditions in the regulation of intertidal hydroid communities on boreal rocky shores.

The spatial distribution pattern of the epiphytic hydrozoan *D. pumila* on the intertidal alga *Ascophyllum nodosum* was studied in adjacent wave-sheltered and wave exposed areas (Rossi *et al.* 2000). Although there was no significant difference in abundance between these areas, *D. pumila* was more abundant on the basal and apical sections of the algae than on the central

sections. The proportion of *D. pumila* hydrothecae that contained hydranths was close to 100% in the sheltered area compared to 70% in the exposed area.

Hooper (1997) identified *Dynamena* spp. and *C. multicornis* as key organisms of the biota assemblage associated with the "periwinkle/rockweed" habitat that he described as a type of marine coastal habitat of Newfoundland and Labrador. Hooper (1997) referred to them as "rockweed hydroids", indicating the preferred substrate for attachment. Physical characteristics of this habitat type often include hard substrates (bedrock, boulders and stable, coarse gravel), protection from major ice scour and low to moderate exposure to wave energy.

The spatial distribution pattern of the epiphytic hydrozoan *C. multicornis* on the intertidal alga *A. nodosum* was also studied in adjacent wave-sheltered and wave exposed areas (Rossi *et al.* 2000). *Clava* were more abundant on the wave-sheltered algae than on the exposed algae and the number of hydranths per colony of *Clava* was also higher.

Relation to Man

Numerous species of cnidarians are predators of the ichthyoplankton of commercially important fish species. In addition to this impact, some hydroids are direct competitors with commercial fish species for the same prey (e.g., copepods). Hydroids may also be a food source for some fish species.

3.1.2 Jellyfish (*Cyanea capillata*; *Aurelia aurita*)

General Information

The planktonic medusa is the dominant and conspicuous stage in the life cycle of jellyfish (scyphozoans), while the sessile polyp is restricted to a small larval stage. These cnidarians are typically dioecious. The fertilized eggs develop into planulae, ovoid ciliated larvae that settle to the ocean bottom after a brief free-swimming existence. The planulae require hard, stable substrates for attachment purposes. The attached planulae then develop into small polypoid larvae called scyphistomae, which subsequently give rise to young medusae (ephyrae) through various processes that are species-specific. The near microscopic ephyrae eventually break free from the oral end of the scyphistomae and feed largely on small crustaceans. They may take six months to two years to reach sexual maturity, are generally < 10 mm in diameter and either lack tentacles completely or have a reduced number. While most scyphozoans have both pelagic and benthic aspects to their life cycles, some species exhibit only one or the other stage (Barnes 1980).

Jellyfish occur both inshore and offshore. Substantial amounts of jellyfish (unspeciated) have been caught during the plankton and nekton surveys on the northeast Newfoundland Shelf and Grand Banks since 1994. During late August to early September 1998, jellyfish were quite widespread inshore all along the northeast coast and Avalon portions of the study area, as well as offshore, particularly in the northern and central portions of the Grand Bank. The highest catches of jellyfish were made at night (Dalley *et al.* 1999). Two common jellyfish species that occur in Newfoundland and Labrador waters are *Cyanea capillata* and *Aurelia aurita*.

Information Specific to *Cyanea capillata* and *Aurelia aurita*

Cyanea capillata (Lion's Mane or Red Jelly): This is the largest jellyfish in the world and occurs in the northwest Atlantic Ocean from Labrador to Cape Hatteras. The bell diameter of this species can be as much as 2 m. This jellyfish species appears in swarms in the northern part of its range during late spring/summer and the presence of large individuals may persist into the fall. These animals may be found in bays and sounds and offshore in the open ocean (Gosner 1979).

This jellyfish requires relatively warm water and higher salinity levels associated with deep water. Brewer (1991) studied this jellyfish in Connecticut during February to September, 1974 to 1989. The surface temperature and salinity ranges during the times medusae were present in the bay were 6 to 25 °C and 24 to 33 ppt, respectively. Martinussen and Baamstedt (2001) investigated the effect of temperature on digestion and swimming activity of *C. capillata* ephyrae. The water temperature range used in the study was 5 to 20 °C. They found that the highest pulsation rate of the ephyrae occurred in the 10 to 15 °C range and that digestion time decreased with increasing temperature. *C. capillata* occurred only in the near bottom zone at deepwater stations during August in the southern Baltic Sea (Herra 1988). In the Baltic Sea in late July-early August, Margoński and Horbowa (1994) also found *C. capillata* at depths of 50 to 70 m and water temperatures ranging from 4 to 12 °C.

Summertime predation on zooplankton by large jellyfish, including *C. capillata*, was studied *in situ* in Alaskan waters during the late 1990s (Purcell 2003). The diet consisted mainly of copepods, larvaceans, cladocerans and variety of meroplankton. Generally, few eggs and larvae were found in the gut contents. Purcell (2003) calculated that individual medusae consumed hundreds to thousands of prey daily. *C. capillata* ate mostly larvaceans, its diet being most similar to a hydromedusan species (Purcell and Sturdevant 2001). Purcell and Sturdevant (2001) concluded that the diets of pelagic coelenterate and forage fish species in Prince William Sound overlap substantially and that the species co-occur spatially and temporally. The authors felt that there is potential for the zooplanktivore groups to compete for food.

De Lafontaine and Leggett (1988) conducted predation experiments using *in situ* enclosures during three summers in Bryant's Cove, Newfoundland. *C. capillata* and *A. aurita* were both tested as potential predators of larval Capelin. They concluded that macroinvertebrate predation has the potential to be a primary regulator of fish larval survival. During the survey in the Baltic Sea, *C. capillata* was found where cod eggs were abundant, in the 50 to 80 m layer of the water column (Margoński and Horbowa 1994). The authors pointed out the potential of this jellyfish to be an important predator on fish eggs occurring in the same strata. Hansson (1997) described the predation upon *A. aurita* by *C. capillata* in waters off Sweden.

Aurelia aurita (Moon Jelly): The northwest Atlantic Ocean distribution of this often studied jellyfish species extends from Greenland to the West Indies, but is relatively rare south of Cape Cod (Gosner 1979). Examination of the extensive literature reveals three striking features: (1) the presence of populations in a wide range of environmental conditions; (2) large inter-population differences in abundance and life history patterns over large and small spatial scales;

and (3) inter-annual variability in various aspects of its population dynamics (Lucas 2001). Thus, this jellyfish is highly adaptable to a wide range of environmental conditions.

The pattern of development of this medusan is characterized by a dormant phase in winter, followed by rapid growth in spring and early summer (Möller 1979). Miyake *et al.* (1997) reported that planulae appear in Japanese waters during early to mid-spring. *A. aurita* can tolerate salinities as low as 16 ppt (Gosner 1979). *A. aurita* occurred primarily in the nearshore zone during August in the southern Baltic Sea (Herra 1988), an indication of its tolerance of lower salinities. Watanabe and Ishii (2001) suggested that ripe medusae with planula larvae occur throughout the year in Tokyo Bay. Moon jellies were sampled from a well mixed area within a 1 to 3 m depth range where salinities ranged from 21.5 to 26 ppt and temperatures varied between 4.1 and 10.1 °C (Sullivan *et al.* 1997b).

The distribution of *A. aurita* in the Black Sea was investigated to depths of up to 200 m during summer, winter and spring between 1991 and 1995 (Mutlu 2001). The Moon Jelly occurred primarily in the upper part of the mixed layer (depth range of 20 to 40 m) during both day and night. Some were found in the cold intermediate layer where water temperatures were less than 8 °C and dissolved oxygen was relatively high. Release of ephyrae occurred in the spring when water temperatures were between 11 and 12 °C.

While eutrophication of marine waters often results in a decrease in the diversity of pelagic coelenterates, it appears that the biomass of certain species may increase. Arai (2001) concluded that the species which most often survive and may also increase in biomass are holoplanktonic or shallow water forms. *A. aurita* seems to be one such species.

A four-year study conducted off Rhode Island during the March to April period indicated the importance of relatively large prey (> 1 mm) in the diet of young medusae (ephyrae) of the Moon Jelly (Sullivan *et al.* 1997b). Rotifers were the only small prey consumed in quantity and only when they were abundant in the plankton. Their frequencies of occurrence in the guts of the ephyrae were clearly related to their abundance in the plankton. Although copepod nauplii were the most abundant prey in the plankton, they were not readily ingested by *A. aurita.* Hydromedusae were present in the gut contents even when at low abundance in the plankton. There were implications that habitats providing even low abundances of large gelatinous species like hydromedusae (hydrozoans) or larval ctenophores might support maximal growth of ephyrae.

Using video methods, Costello and Colin (1994) determined that the tentaculate Moon Jellies created fluid motions during swimming which entrained prey and brought them into contact with the tentacles. They predicted that *A. aurita* would select zooplankton and hydromedusae whose escape speeds were slower than the flow velocities generated at the bell margins. In other words, prey type and size varied between Moon Jelly medusae of varying bell diameter since flow field velocity is a function of bell diameter (Costello and Colin 1994; Sullivan *et al.* 1994).

Martinussen and Baamstedt (2001) investigated the effect of temperature on digestion and swimming activity of *A. aurita* medusae. The water temperature range used in the study was 5 to 20 °C. The authors reported that the pulsation rate of this gelatinous planktivore increased

linearly with increasing temperatures and that digestion time decreased with increasing temperature.

Båmstedt *et al.* (2001) studied the growth of newly released *A. aurita* ephyra larvae fed five different food types, including a large copepod, a phytoflagellate and suspended particulate organic matter made from bivalve meat. They concluded that ephyrae of this species can capture and feed on phytoplankton, large copepods and particulate organic matter. They also concluded that phytoplankton could be of nutritive significance during early development and that large copepods are inefficiently converted to growth during early development. The authors also concluded that particulate organic matter is a potential food source but that its effect on growth is dependent on its concentration, size distribution and nutritional composition.

Matsakis and Conover (1991) sampled the upper 30 m of the water column in Bedford Basin, Nova Scotia between March and June. In addition to five hydromedusan species and one ctenophore species, the scyphomedusan *A. aurita* was collected. In May and June, the moon jellies could be seen at the surface. Moon Jelly guts sometimes contained more than twenty prey items, including copepods, copepod nauplii, ctenophore eggs, chaetognath eggs, fish eggs, veligers (mollusc larvae), fish larvae, hydromedusae and microplankton. *A. aurita* may significantly reduce larval fish and copepod populations.

Work carried out by Purcell (2003) on summertime predation on zooplankton by large jellyfish in Alaskan waters during the late 1990s included a jellyfish in the genus *Aurelia* (*A. labiata*). The diet of this jellyfish consisted mainly of copepods, larvaceans, cladocerans and a variety of meroplankton. *A. labiata* ate mostly crustacean prey, its diet being most similar to a ctenophore species and to juvenile Walleye Pollock, Sand Lance and herring (Purcell and Sturdevant 2001). Purcell and Sturdevant (2001) concluded that the diets of pelagic coelenterate and forage fish species in Prince William Sound overlap substantially and that the species co-occur spatially and temporally. The authors felt that there is potential for the zooplanktivore groups to compete for food.

Gut content analyses on field-caught *A. aurita* from the Gulf of Mexico showed both quantitative and qualitative change in diet as a function of medusa size (Graham and Kroutil 2001). Larger medusae tended towards greater numbers and diversity of prey, possibly a means to enhance diet which in turn may positively influence growth and reproduction.

During a survey in the Baltic Sea in late July-early August, Margoński and Horbowa (1994) found *A. aurita* at depths of 50 to 60 m and since cod eggs were abundant in the 50 to 80 m depth range during the survey, this indicated the potential for this jellyfish to be an important predator on fish eggs occurring in the same strata. Behrends and Schneider (1995) also concluded from their work in the Baltic Sea that *A. aurita* directly impacts mesoplankton community composition. Schneider (1993) concluded that predation by *A. aurita* probably has higher impact in nearshore areas than in the offshore areas. Båmstedt (1990) suggested that natural populations of *A. aurita* probably exploit patches of highly abundant prey and are otherwise food limited.

Relation to Man

Many scientists believe that jellyfish play very significant roles in marine planktonic ecology. Jellyfish feeding on fish eggs and larvae probably represents the greatest impact on human activity. As mentioned, there is speculation that certain year classes of particular fish species populations have been reduced by these animals' feeding habits. Low abundances of fish eggs and larvae have been found in areas where *A. aurita* were most numerous, a possible indication of this animal's predatory impact (Herra 1988). Thus, there are possible implications of increases in jellyfish biomass for the ecosystem. (Brodeur *et al.* 2002). Jellyfish are an important food source of the Leatherback Sea Turtle (*Dermochelys coriacea*), a species at risk (Government of Canada 2010).

The world jellyfish fishery occurs mainly for export to Japan and to a lesser extent Singapore, Hong Kong and Taiwan. There is an *A. aurita* fishery in southern British Columbia (Sloan and Gunn 1985) and potential for such a fishery has been explored in Newfoundland and Labrador (Government of Newfoundland and Labrador 2002).

3.1.3 Sea Anemones (*Metridium senile*; *Urticina felina*)

General Information and Life Cycle

Anthozoans are either solitary or colonial polypoid cnidarians which do not have a medusoid stage in their life cycles. Although polypoid, sea anemones differ considerably from hydroids in many respects (Barnes 1980). Sea anemones are solitary polyps that are considerably larger and heavier than hydroids. The major part of the sea anemone body is comprised of a heavy column. A flattened pedal disc for attachment to the substrate is located at the aboral end of the column and at the oral end, the column flares slightly to form the oral disc which bears the tentacles. The mouth is located in the center of the oral disc (Barnes 1980).

Sea anemones are either hermaphroditic or dioecious, with fertilization occurring in either the gastrovascular cavity or in the outside seawater. Planulae that hatch from the fertilized eggs are either planktotrophic or lecithotrophic and have variable development times. Eventually the developed planulae settle, attach to a substrate and form tentacles (i.e., develop into adult form) (Barnes 1980). Two sea anemone species that are common to Newfoundland and Labrador waters are *Metridium senile* and *Urticina felina.*

Information Specific to *Metridium senile* and *Urticina felina*

Metridium senile (Frilled Sea Anemone): This species is distributed in the northwest Atlantic Ocean from the Arctic to Delaware Bay. It inhabits a range of depths from the intertidal zone to 150 m and is eurythermic (< 5 °C to > 15 °C). The Frilled Sea Anemone is the most common and largest anemone within its range, often occurring on wharf pilings, in rock crevices and tidal pools. The height of this species ranges up to approximately 100 mm with smaller individuals occurring in shallow water (Gosner 1979).

M. senile reproduces sexually by shedding eggs and sperm into the surrounding water where external fertilization occurs and development proceeds according to the general anthozoan life cycle already described (Widersten 1968; Bucklin 1982). In areas with low salinity, *M. senile*

colonizes by means of locomotion and/or asexual reproduction/laceration rather than by sexual reproduction and pelagic larvae (Wahl 1985). *M. senile* is described as "hemisessile" because of its capability of restricted locomotion.

Hooper (1997) identified *M. senile* as one of the key animals in the biota assemblage associated with "sea urchin barrens" habitat that he described as a type of marine coastal habitat in Newfoundland and Labrador. Sea urchin barrens are areas where macroalgae have been almost completely eliminated due to excessive herbivory from high densities of sea urchins (Lawrence 1975). Physical characteristics associated with this habitat type included bedrock/boulder substrates, full salinity, some current effect, resilience to ice scour and moderate to full exposure to wave energy (Hooper 1997). Himmelman (1991) found the Frilled Anemone to be common in the upper part of the filter feeders zone of subtidal communities in the northern Gulf of St. Lawrence. The onset of this zone tended to coincide with a decrease in sea urchin abundance.

Himmelman *et al.* (1983) found *M. senile* at all depths sampled (1 to 5.5 m) in a rocky subtidal zone in the St. Lawrence Estuary. The summer distribution of *M. senile fibriatum* in the Sea of Japan rocky sublittoral area at depths of 2 to 15 m was recently investigated in relation to abiotic environmental factors (Tkachenko and Zhirmunsky 2002; Tkachenko 2003). The study found that the distribution of this sea anemone was significantly dependent on the intensity of water exchange and bottom slope. The largest aggregations of *M. senile fibriatum* were found at depths exceeding 10 m on vertical walls located at acute angles or parallel to the prevailing directions of wave flows and in shallow gaping crevices with a stable direction of water flow. Sea anemones were sampled from 30 to 35 m depths at both inshore and offshore locations in the Gulf of Maine (Lesser *et al.* 1994). Whomersley and Picken (2003) studied the long-term dynamics of fouling communities found on offshore installations in the North Sea. Although not dominant as a primary colonizer, *M. senile* tended to dominate the region below the lower limit of the mussel zone (~ 30 m) down to depths ranging from 80 to 140 m by year 3 or 4.

During a study on the effects of food availability and water flow on the physiological ecology of *M. senile*, Lesser *et al.* (1994) found that inshore populations of the Frilled Sea Anemone in the Gulf of Maine had a lower scope for growth than offshore populations, despite the higher mean concentrations of particulate organic matter inshore. They concluded that the flux of seston appears to be an important factor affecting the performance of a passive suspension feeder. Bucklin (1987) reported that individual *M. senile* in the intertidal zone are growth limited by food availability, feeding time duration and damage from wave exposure while those on floats, for example, grow much larger.

The abundance and size-distribution of *M. senile* in relation to dredging activity and flow velocity was recently studied in Denmark (Riis and Dolmer 2003). There was a lower density in the dredged area compared to the undisturbed area, but the mean individual size was greater in the dredged area. Riis and Dolmer (2003) hypothesized that the quantity and quality of the substrate determines the density and size of *M. senile*. They concluded that because of the paucity of shell debris at the dredged area, the movements of the sea anemones were restricted as were their ability to reproduce asexually. Therefore, the energy at the dredged area was allocated into individual growth. With respect to flow velocity, the authors reported that higher densities of *M. senile* were found at areas with the highest flow rates.

With respect to feeding, *M. senile* intercepts prey from the water column with its tentacles and then transfers the prey to its mouth (Sebens 1981). Frilled Sea Anemones on subtidal New England rock walls at depths no greater than 16 m fed primarily on crustacean and larval zooplankton (Sebens and Koehl 1984). Specific items included barnacle cyprids, ascidian larvae and gammaridian amphipods, all within a 400 to 1,000 µm size range. Being a passive suspension feeder, *M. senile* depends on substrate related prey (i.e., demersal zooplankton and benthic material washed off the substrate by currents). Shick and Hoffmann (1980) found that intertidal *M. senile* in Maine grew larger in microhabitats with moderate to high tidal currents than in adjacent microhabitats with less water movement. The size of this sea anemone tends to increase with depth (Anthony and Svane 1994). Abutrab (1992) investigated particle clearance rates of *M. senile* collected off Logy Bay, Newfoundland and Labrador and found that anemones showed a preference for larger particle sizes (> 47 µm diameter), especially algae and rotifers.

M. senile is also an important prey species. The most abundant invertebrate prey item found in Winter Flounder collected in eastern Newfoundland between June and August was *M. senile* (Keats 1990). This sea anemone accounted for over 10% of the flounder diet by weight (17% of identifiable items) and occurred in 39.3% of the stomachs containing food. All fish were taken from hard substrates dominated by sea urchins at depths ranging from 5 to 15 m, typical of the open Atlantic coast of Newfoundland.

*Urticina (*formerly *Tealia) felina* (Northern Red Sea Anemone): Gosner (1979) indicated that this wide-ranging, sexually reproducing, boreal sea anemone is generally found in the intertidal zone from the subarctic to Casco Bay, Gulf of Maine. He added that this species is sometimes found as far south as Cape Cod, but only in the subtidal zone.

Logan (1988) undertook photographic sampling of a sublittoral hard substrate epibenthic community between depths of 30 and 140 m in the Bay of Fundy, New Brunswick. His study indicated a gradual but significant increase in the abundance of *Urticina felina* with increasing depth. The approximate density of Northern Red Sea Anemones at 135 to 150 m was $54/m^2$, while the density of these anemones was just under $4/m^2$ at 30 to 45 m depth. During this study, the salinity over the depth range was consistent between 30 and 32 ppt, but water temperatures were more variable (0.5 to 14.0 °C). The area was steep-sided and the substrates, relatively free of fine sediments, consisted primarily of gravel and shell patches. Logan (1988) detected significant water movement along the bottom, approximately 1 m/s at the 17 m depth.

Himmelman (1991) also observed an increase in the Northern Red Anemone with increasing depth during his SCUBA observations of subtidal communities in the northern Gulf of St. Lawrence. The anemones tended to occur at the lower end of the filter feeders' zone that was located below the algal and sea urchin barrens zones. He observed this predatory anemone feeding on dislodged sea urchins on rocky faces. Himmelman *et al.* (1983) found *U. felina* primarily at depths of 4 m or more in a rocky subtidal zone in the St. Lawrence Estuary. Individual heights typically range from 25 to 65 mm, with the larger anemones occurring in deeper water.

Hooper (1997) identified *U. felina* as one of the key animals in the biota assemblage associated with "sea urchin barrens" habitat that he described as a type of marine coastal habitat in

Newfoundland and Labrador. Physical characteristics associated with this habitat type included bedrock/boulder substrate, full salinity, some current effect, resilience to ice scour and moderate to full exposure to wave energy (Hooper 1997).

Relation to Man

Although neither of these sea anemone species is used as a food source for man, they are being used in other capacities. There is some indication that the white form of *M. senile* could serve as a biological indicator for ultraviolet radiation. Westholt *et al.* (2001) showed that long-term exposure to ultraviolet radiation caused numerous irreversible changes to this sea anemone, including body-mass reduction, escape behaviour (relocation) and pigmentation shift. Koehl (1999) discussed the role of *M. senile* in biomechanical research. He illustrated how ecological studies can enhance or change our understanding of biomechanical issues. Mercier *et al.* (1998) used *M. senile* specimens from the St. Lawrence Estuary to gather realistic data on the response of widespread marine organisms toward tributyltin contamination and thus provide additional information regarding the impact of this persistent contaminant on coastal marine ecosystems.

3.2 CTENOPHORA

3.2.1 Comb Jellies (*Pleurobrachia pileus*; *Bolinopsis infundibulum*)

General Information

Comb jellies, also known as ctenophores, exhibit direct development, meaning they do not have distinctive larval and sessile stages. They are voracious predators, exhibiting cannibalistic behaviour and predation on other zooplankton species. Like many plankters, these marine animals often occur in swarms. In general, comb jellies are common inshore and in estuaries, but will move to deeper water during rough sea conditions (Gosner 1979).

All ctenophores are hermaphroditic. The eggs and sperm are usually shed to the exterior through the mouth and fertilization occurs in the water column. Exceptional species brood their eggs. The fertilized egg develops into a free-swimming cydippid larva that closely resembles an adult ctenophore (Barnes 1980). Two comb jelly species that occur in Newfoundland waters are the Sea Gooseberry (*Pleurobrachia pileus*) and the Common Northern Comb Jelly (*Bolinopsis infundibulum*).

Information Specific to *Pleurobrachia pileus* and *Bolinopsis infundibulum*

Pleurobrachia pileus (Sea Gooseberry): Gosner (1979) reported that this species occurs year round from the Bay of Fundy south to North Carolina. Bay of Fundy specimens are typically 20 to 30 mm in diameter but are smaller southward. It is confined to inshore waters during the winter, but ranges further offshore during summer and fall when it reaches peak abundance. The Sea Gooseberry is seldom found in estuaries. However, Wang *et al.* (1995) described the spring abundance and distribution of *Pleurobranchia pileus* in the Seine Estuary, France. The ctenophores displayed passive tidal advection and active diel vertical migration. Many individuals remained aggregated near the bottom at all times, perhaps behaviour intended to avoid tidal advection out of the estuary.

The distribution of this ctenophore coincided with the 33 and 15 ppt isohalines, with high abundances occurring on the marine side of the estuary (Wang *et al.* 1995), although these euryhaline creatures have been found in natural salinities as low as 7 ppt and as high as 35 ppt. Laboratory experimentation (Greve 1973) revealed a tolerance range of 12 to 45 ppt. Rapid salinity changes of 2 to 3 ppt appeared to affect the normal behaviour of this ctenophore.

Frank (1986) suggested that surface waters (upper 20 m) are the preferred depth zone for this species and that their depth of occurrence remained the same regardless of seasonal thermal stratification. Other results have shown otherwise. Greve (1973) indicated that this species tended to avoid surface turbulence. Sampling in the Black Sea between 1996 and 1999 provided data on the spatial and temporal distributions of *P. pileus* (Kideys and Romanova 2001). In the Black Sea, it was mainly concentrated below the mixed water layer (below 20-25 m depth) in the deep, offshore waters. *P. pileus* also displayed low inter-annual variation in its distribution over a four-year period. Gardner and Howell (1983) and Anderson and Gardner (1986) found that the shallow water shelf zooplankton community of the Southeast Shoal, Newfoundland Grand Banks, in May 1981 was dominated by gelatinous zooplankters, particularly *P. pileus*. Depths where Sea Gooseberries dominated the zooplankton ranged from 50 to 60 m. During work on Georges Bank, Norrbin *et al.* (1996) found that *P. pileus* were most abundant in stratified waters of 80 to 90 m, compared to well mixed waters 40 to 45 m deep and slope waters at 140 to 160 m. Gallager *et al.* (1996) also found *P. pileus* to be most abundant at about 70 m on Georges Bank in May, although some of these animals were sampled at 30 to 40 m depths.

Greve (1973) collected Sea Gooseberries from German waters and conducted laboratory experiments to investigate the effects of environmental parameters on this ctenophore. He found that these ctenophores were naturally distributed in German waters over annual isotherms ranging from 4 to 21 °C. Two individuals released eggs at 12 °C. One released approximately 4,000 eggs and the other about 7,000 eggs. After 48 hours, 50% hatch occurred from eggs held at 13 °C and 75% hatch occurred from eggs held at 18 °C. In the laboratory, he found that the Sea Gooseberries commenced downward vertical migration once the water temperature reached about 24 °C, apparently in search of cooler conditions. At 26 °C, 50% of the animals died within 24 hours. *P. pileus* subjected to 0 °C temperatures for 24 hours showed no apparent damage, although there was a reduction in the comb beating that resulted in ctenophore sinking.

The population dynamics and feeding ecology of this ctenophore were investigated during two spring periods on Browns Bank, southwestern Scotian Shelf, in areas with 90 to 100 m depths and relatively weak currents. Frank (1986) was hoping to resolve the uncertain ecological status of *P. pileus* in the offshore pelagic food web. The timing of the investigation was set to coincide with spawning by cod and haddock. Large crustacean zooplankton (> 1 mm), principally copepods, were the dominant prey in the comb jelly's diet, accounting for an average of 70% by weight of total prey consumed, regardless of ctenophore size. A non-selective, density dependent pattern of prey exploitation by this ctenophore was indicated. Fish eggs and *Oikopleura* sp. were found in less than 2% of the Sea Gooseberries examined despite the high concentration of fish eggs in the upper water column. Fish larvae were completely absent in the diet. Frank (1986) suggested that extremely low levels of haddock larvae produced on Browns Bank during one of the years when ctenophore density was highest resulted from food shortages induced by the high level of predation on zooplankton by *P. pileus*.

Interactions between *P. pileus*, copepods, ciliates and phytoplankton were studied experimentally in Sweden in 1990 to investigate whether manipulations of ctenophore and mesozooplankton abundance could change the phytoplankton biomass and species composition of a natural late spring phytoplankton community (Granéli and Turner 2002). Results indicated that the primary top-down effect of ctenophore predation on copepods was to reduce copepod predation on ciliates, thereby increasing ciliate grazing on the small flagellates that dominated the phytoplankton.

Sea Gooseberries seem to prefer feeding on actively swimming organisms (Greve 1973) and prey is captured by adhesion to the tentacles (Gosner 1979). One aspect of their ecological significance pertains to their direct competition with fish larvae for zooplankton prey. Milne and Corey (1986) reported a distributional pattern of *P. pileus* in the Bay of Fundy region between 1975 and 1982 that was similar to that recorded for larval herring. Their study indicated that spawning had started by July (samples contained predominantly young ctenophores), but spring samples did not show any evidence of spawning. Suthers and Frank (1990) aimed to determine the extent to which the spring horizontal distribution of zooplankton was influenced by ctenophores. Their work suggested that reduced growth by post-larval cod off southwestern Nova Scotia during 1985-1987 might have been associated with ctenophore predation of a common prey resource, in this case zooplankton larger than 1,050 µm. Arai *et al.* (1993) also described predation by *P. pileus* on copepods in direct competition with numerous ichthyoplankton off Vancouver Island.

Common predators of Sea Gooseberries include mackerel, Spiny Dogfish (Alonso *et al.* 2002) and other fishes (Gosner 1979). Greve (1973) identified lumpfish (*Cyclopterus lumpus*) as a predator of this ctenophore. Östman (1997) suggested that *P. pileus* might be an important prey item of *Aurelia* and *Cyanea* scyphopolyps in sheltered shallow areas during certain times of the summer in Sweden.

Bolinopsis infundibulum (Common Northern Comb Jelly): This comb jelly species ranges from the Arctic to Cape Cod in the northwest Atlantic Ocean and is most common during April to September. These animals can reach lengths of 150 mm (Gosner 1979). Information regarding the biology and distribution of this animal is scarce given its extreme delicate nature.

Norrbin *et al.* (1996) found that *Bolinopsis infundibulum* were more abundant in stratified waters of 80 to 90 m than in well mixed waters 40 to 45 m deep and slope waters at 140 to 160 m. Off northern Norway, Falkenhaug (1996) observed an increase in the biomass of *B. infundibulum* during April and May in surface waters (upper 20 m). Reproduction by this ctenophore continued throughout the summer months. By August, the biovolumes of *B. infundibulum* began to decrease, leaving a small number of individuals to overwinter. In Sweden, Bergström *et al.* (1990), that this ctenophore was most abundant at discontinuity layers in the water column. They observed this at a halocline of 15 m, a thermocline/slight halocline at 50 m and just over the ocean bottom at 110 m. The highest density was at the 15 m halocline. A dense occurrence of *B. infundibulum* was observed at a depth of approximately 1250 m near the seafloor off Japan (Toyokawa *et al.* 2003) where many of the ctenophores were in a foraging posture. The authors speculated that these ctenophores were feeding on epipelagic copepods that were sinking to the sea bottom during diapause.

Matsumoto and Harbison (1993) used direct observation to study the foraging and feeding behaviours of *B. infundibulum* during a summer off the U.S. east coast. They found that the Common Northern Comb Jelly forages vertically, capturing prey with mucus-covered oral lobes. Falkenhaug (1996) observed predation on *B. infundibulum* by another ctenophore species, *Beroe cucumis*.

Sornes and Aksnes (2004) examined the effects of instantaneous predation efficiency and light dependency on the competition between the tactile predator *B. infundibulum* and one of its visual predator competitors. They found that the predation rate of *B. infundibulum* was proportional to prey density and that changes to the light levels had no significant impact on the feeding pattern of this ctenophore. The authors concluded that as visibility decreases and prey density increases, the competitive efficiency of tactile predators, such as *B. infundibulum*, increases.

Relation to Man

Although neither of these two comb jelly species is important to man as a food source or as specimens in biomedical research, they are important organisms from an ecological perspective. Purcell and Arai (2001) reviewed the information on interactions of ctenophores with fish. The interactions that could be potentially detrimental to fish populations include predation by ctenophores on pelagic eggs and larvae of fish, competition for prey with fish larvae and zooplantivorous fish species and ctenophores acting as intermediate hosts for fish parasites. Identified interactions that are positive for fish include predation on gelatinous species by fish and commensal associations among fish and ctenophores. As fishing pressure increases, it becomes more important to understand the ecological relationships between pelagic coelenterates and fish.

3.3 MOLLUSCA

3.3.1 Periwinkles (*Littorina littorea*; *Littorina obtusata*)

General Distribution

The Common Periwinkle (*Littorina littorea*) is widely distributed throughout the North Atlantic Ocean. In the northwestern Atlantic Ocean, this gastropod occurs from Labrador to New Jersey, from the high water mark to depths of 40 m on diverse substrates ranging from rock to sand (DFO 1998a). This species is very characteristic of the intertidal zone and is generally the most dominant molluscan species in the mid-intertidal zone.

The Smooth Periwinkle (*Littorina obtusata*) is also distributed on both sides of the Atlantic Ocean. In the northwestern Atlantic Ocean, it occurs from the Arctic to New Jersey and is commonly found among rockweeds (Gosner 1979). Its local distribution is limited by its requirement for rockweed, sheltered rocky coasts and clear water.

Both of these periwinkle species have been identified as key animal species of the biota assemblage often associated with the "periwinkle/rockweed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat for Newfoundland and Labrador. Physical characteristics of this habitat type include hard bottom substrates (bedrock, boulders and stable coarse gravel), reduced to full salinities, protection from major ice scour and low to moderate

exposure to wave energy (Hooper 1997). Mann (1992) described the roles of these two species in intertidal rockweed bed communities in the Bay of Fundy.

Golikov and Scarlato (1973) reported temperature conditions of existence, optimum temperatures of inhabitancy and spawning temperatures for these two members of the "Atlantic-boreo-subtropical species" group. The summer and winter temperatures for the northern boundary of its distributional area were 6 and < 0 °C, respectively and the summer and winter temperatures for the southern boundary of its distributional area were 20 and 16 °C, respectively. The ranges of optimum temperatures of inhabitancy and spawning were given as 6 to 16 °C and 4 to 16 °C, respectively.

Life Cycle

Spawning and Fertilization: The Common Periwinkle and the Smooth Periwinkle are both dioecious. The Common Periwinkle typically releases its fertilized eggs into the plankton during the spring/early summer period (April to July) (Hayes 1929), while the Smooth Periwinkle lays its fertilized eggs on the fronds of rockweed species (*Fucus* spp.) (Barkman 1955).

Chase and Thomas (1995) found that varying the rate or onset time of water temperature increase influenced the timing of peak spawning and the duration of spawning by *L. littorea*. An accelerated temperature increase caused peak spawning to occur three weeks earlier than normal and shortened the duration from 21 weeks to 14 weeks. In New Brunswick, Chase and Thomas (1995) found that gonad maturation occurred from January to April and copulation occurred in late April-early May, while water temperatures were approximately 5 to 6 °C. Maximum spawning occurred when water temperatures approached 10 °C.

Fertilized Eggs and Larvae: Of the nineteen recognized species of the snail *Littorina*, nine show pelagic larval development and the other ten have direct, non-pelagic development. Species with pelagic development always have a distinct reproductive season, while species with non-pelagic development either reproduce throughout the year or show variation between regions in seasonal or non-seasonal reproduction (Erlandsson 2002).

L. littorea – In the Common Periwinkle, fecundity is positively correlated with shell spire height (Chase and Thomas 1995). Chase and Thomas (1995) estimated that a female with a 27 mm high spire would produce approximately 113,000 fertilized eggs/embryos per season. The fertilized eggs of the Common Periwinkle are often found in nearshore plankton. The developing embryos of this species cannot survive salinities less than 10 ppt and they require a salinity of at least 20 ppt for normal development (Hayes 1929). The free-swimming larvae (veligers) hatch approximately six days after fertilization (Caddy *et al.* 1974). The larvae appear to have salinity tolerances similar to that of the developing eggs/embryos (Hayes 1929). Common Periwinkle larvae remain planktonic for up to 4 weeks and then settle to the bottom. Their dispersion is highly dependent on oceanic currents.

L. obtusata - Fertilized eggs of the Smooth Periwinkle are usually lightly attached to algae of the genera *Ascophyllum* (knotted wrack) and *Fucus* (rockweed) growing in sheltered locations. The

upper limits of water temperature and salinity tolerances of Smooth Periwinkle eggs are approximately 26 °C and 25 ppt, respectively (Barkman 1955).

Juveniles and Adults:
L. littorea - Common Periwinkle juveniles and adults appear to prefer rocky shore habitat at and below mean low water (Gendron 1977). Mann (1992) stated that *L. littorea* individuals are normally concentrated in the lower area of the intertidal zone. They are eurythermal and euryhaline (Gardner and Thomas 1987). Their preferred water temperatures are approximately 18 °C and their upper limit of water temperature tolerance is around 41 °C (Hayes 1929). The Common Periwinkle is relatively inactive once water temperatures exceed 25 °C (Caddy *et al.* 1974). Loomis (1995) reported that this periwinkle is able to withstand temperatures as low as –13 °C in winter and its minimum lethal temperature in the summer is –11 °C; however, its freezing tolerance is increased if it is acclimated to high salinity. This periwinkle species is able to tolerate salinities as low as 13 ppt and, therefore can exist at the head of estuaries. This periwinkle species can tolerate the full ranges of exposure to wave energy and currents. Clarke *et al.* (2000) examined the effects of acclimation, previous thermal history and size on the thermal tolerance of Common Periwinkles collected in England. In particular, they studied the nature of "heat coma" in this periwinkle. They found that periwinkles acclimated at temperatures of 16 and 20 °C showed higher tolerances to temperature increases than those acclimated at 12 °C (3 to 5.8 °C upward shift). In terms of thermal history, those periwinkles subjected to repeat heat coma events on a daily basis showed significant declines in coma-temperature, while others exposed to heat coma events on a weekly basis showed no decline in thermal tolerance. Clarke *et al.* (2000) also found that large periwinkles (> 20 mm shell length) were more likely to show decreased heat tolerance compared to smaller individuals. They also found that low salinity caused a significant decline in thermal tolerance.

Aggregations can be found on subtidal drift algae, in tide pools and along rock crevices. During the winter, the Common Periwinkle population migrates down the intertidal zone to about the mean low tide mark and then returns to the higher intertidal area around March. Petraitis (1982; 1983) conducted field experiments on the movements of the Common Periwinkle and concluded that directional movement by this species is initiated by dislodgement and is modified by the periwinkle's intertidal origin and placement. The optimal habitat of the Common Periwinkle is the substrate under algal canopy or the immediate subtidal. It is often associated with rockweed (DFO 1998a).

The abundance and size distribution of *L. littorea* were studied in low intertidal and shallow and deep subtidal mussel beds found on sedimentary tidal flats in the North Sea (Saier 2000; 2002). In the low intertidal mussel beds, high densities (> 1,300 individuals m^2) of juvenile periwinkles (< 14 mm carapace length (CL)) were positively correlated with barnacle epigrowth on the mussels. Recruitment of *L. littorea* was shown to be restricted to the intertidal zone. Abundances of periwinkles abruptly decreased in the adjacent shallow subtidal zone (< 5 m depth) that appeared to serve as habitat for older snails (> 13 mm CL). *L. littorea* was completely absent from the deep subtidal zone (> 5 m). The intertidal mussel beds appeared to serve as nursery areas for the periwinkles in this area. Gilkinson and Methven (1991) determined that the abundance of *L. littorea* did not change with increasing depth or distance offshore, although mean shell height increased in the Newfoundland and Labrador region.

Common Periwinkles have two peak periods of growth; early spring and early fall. They usually live to 3 years of age, but can survive as long as 4 or 5 years (Gardner and Thomas 1987). Sexual maturity is reached at approximately 25 mm shell length (Caddy *et al.* 1974).

L. littorea grazes on a wide variety of micro- and macroalgae (e.g., *Ulva* sp., *Enteromorpha* sp., diatoms, encrusting algae, juvenile *Fucus* sp.) and on the early settlement stages of sessile invertebrates (Petraitis 1983; Watson and Norton 1985; Barker and Chapman 1990). Work by Sommer (2000) indicated that benthic microalgal diversity was enhanced by spatial heterogeneity of grazing by *L. littorea*. Algal species richness and evenness also increased with increasing proportions of *L. littorea* in the benthic grazers. Petraitis (1995) showed the opportunistic scavenging behaviour of the Common Periwinkle on mussel tissue and its accelerating effect on the periwinkle growth rate. Petraitis (2002) also demonstrated the effects of intra-specific competition on the growth of this periwinkle. Individuals held in higher density situations exhibited lower average growth than those held at lower densities.

Periwinkle feeding can be influential in structuring benthic communities on hard substrate. Experimental removal of this periwinkle from a protected New England rocky beach resulted in rapid habitat and community changes (Bertness 1984). Its removal resulted in rapid sediment accumulation and the development of an algal canopy that accelerated sedimentation and bound sediment to hard substrate. These changes led to the increased success of species characteristic of soft-sediment habitats (e.g., polychaetes) and decreased the success of hard-substrate organisms (e.g., barnacles, encrusting algae). The effects of surface texture and littorinid grazing and their interactions on the establishment of shallow-water benthic hard-bottom communities in the Baltic Sea were recently investigated in a quantifiable manner (Wahl and Hoppe 2002). Grazing efficiency by *L. littorea* depended on initial rugosity (roughness), with minimal efficiency occurring on surfaces of intermediate rugosity. The authors found that the interaction between various factors made it difficult to predict the outcome of recruitment from single factor effects. It has also been suggested that the grazing activities of the Common Periwinkle on algae might negatively impact mussel recruitment due to the removal of mussel settlement sites on the algae (Petraitis 1990).

Juvenile and adult Common Periwinkles are susceptible to numerous predators including man, fish, waterfowl, crabs and lobsters (DFO 1998a). Barnacle epibionts can also have derogatory effects on the health of periwinkles (Buschbaum and Reise 1999). At the same time, recruits of some barnacles (e.g., *Semibalanus balanoides*) in intertidal zones are strongly influenced by the substantial grazing of *L. littorea* (Buschbaum 2002).

Chemically mediated alarm reactions of the Common Periwinkle were studied in laboratory experiments during summer and autumn and were detected as crawl-out responses (i.e., movements of snails out of the water) (Jacobsen and Stabell 1999). During summer testing, *L. littorea* reacted mostly to chemical stimuli from injured conspecifics and seawater conditioned by crabs that had been fed *L. littorea*. However, during the autumn testing, no significant differences were found in responses to the previously mentioned stimuli or extracts of Horse Mussel and seawater conditioned by crabs that had been fed fish. Crawl-out responses were also significantly greater under dark conditions as compared to experimentation under lighted conditions. The authors concluded that *L. littorea* crawl-out responses are primarily in reaction

to conspecific alarm substances, but under some sort of seasonal effect. They also concluded that these snails may be adapted more to night-active predators.

Interesting studies (Davies and Beckwith 1999; Edwards and Davies 2002) have investigated the functional and ecological aspects of the pedal mucus trails of *L. littorea*. Fresh pedal mucus trails are sticky and can retain food particles *in situ* and therefore, can be subsequently grazed by the periwinkles. This could be an additional benefit from the relatively high energy expended in laying down the mucus trails.

Greenway and Storey (2001) presented an analysis of both seasonal and anoxia-induced changes in the enzyme maximal activities and kinetic properties of *L. littorea* collected in New Brunswick. In general, enzyme activities were higher during the summer (July) than during the fall (November). The effects of anoxia were tissue- and season-specific. Anoxia exposure during November induced a greater number of changes in enzyme maximal activities in the foot muscle than in the digestive gland.

L. obtusata - The juvenile and adult Smooth Periwinkles are most abundant on the mid-shore canopy of knotted wrack and rockweed (Watson and Norton 1987). Mann (1992) stated that *L. obtusata* is generally found throughout the intertidal zone, always on the macroalgae. *L. obtusata* was one of the dominant epibenthic species found in an eelgrass bed located in a Maine estuary (Mattila *et al.* 1999). This species' lowest limit on shore is the extreme low water spring tide mark due to its inability to withstand permanent immersion (Barkman 1955). Smooth Periwinkles are not successful on muddy substrates or in areas receiving sediment deposition. Gilbert *et al.* (1984) described this species occurring on inner intertidal flats near Nain, Labrador.

Juveniles and adults of *L. obtusata* become inactive at about 25 °C, but are able to withstand water temperatures as low as –30 °C. They are unable to tolerate strong surf action but can withstand strong tidal currents. This species is quite sensitive to freshwater and individuals will quickly die if salinity drops to 15 ppt without sufficient acclimation time (Barkman 1955).

Sokolova and Pörtner (2001) showed that adaptation of *L. obtusata* to life at different latitudes and/or shore levels involves constitutive changes in activity levels of key metabolic enzymes. Periwinkles adapted to environments with lower mean temperatures tend to have higher enzyme activities than those from warmer habitats.

Laboratory experimentation has been conducted to examine the effect of water velocity on the growth of *L. obtusata* from both wave exposed and sheltered shore populations (Trussel 2002). Snails from both populations exhibited greater growth under low flow velocity versus high flow velocity conditions. In addition, snails from the wave exposed populations grew more than those from the sheltered populations, regardless of flow velocity conditions. This is an example of countergradient variation, showing genetic and environmental influences acting in opposing directions.

Johannesson and Ekendahl (2002) investigated the reason for gastropod shell colour polymorphism. They speculated whether shell colour frequencies are under selection or owing to random evolutionary processes. Using *L. saxatilis* (a rock-dweller with non-cryptic colours)

and *L. obtusata* (a macroalgal dweller with brown/yellow cryptic coloured shells), they conducted an experiment that suggested selection favouring a colour that matches the background from the perspective of visual predators.

The Smooth Periwinkle prefers to feed on the reproductive receptacles of fucoid algae, but will also feed on the vegetative tissue. Other algal species consumed by this gastropod include *Ulva lactuca* and *Ascophyllum nodosum* (Hunter 1981; Watson and Norton 1987).

Relation to Man

There is a limited periwinkle fishery in eastern Canada. Hand gathering of periwinkles is an open fishery not requiring a license. The Common Periwinkle is a popular food item in Europe (Caddy *et al.* 1974; DFO 1998a). Cummins *et al.* (2002) recently conducted an assessment of the potential for the sustainable development of a *L. littorea* industry in Ireland.

There has also been some investigation into the use of periwinkles (e.g., *L. littorea*) as biomarkers in order to monitor certain aspects of environmental degradation (Galloway *et al.* 2004). Burrows *et al.* (2002) looked at spatial synchrony of population changes in rocky shore communities in Shetland to determine whether some of the dominant species might be good indicators of ecosystem responses to climatic change. They concluded that the periwinkles, including *L. obtusata,* might not be very sensitive to this type of change.

3.3.2 Waved Whelk (*Buccinum undatum*)

Distribution

The distribution of the Waved Whelk in the northwestern Atlantic Ocean extends from Labrador south to New Jersey, including the Gulf of St. Lawrence. This gastropod is very common in cold water from tidal level to depths of 180 m. It occurs in areas ranging from low to high wave energies and low to strong currents (DFO 1997a; Kenchington and Glass 1998). Its greatest densities occur in Labrador, eastern Newfoundland and the northern shore of the Gulf of St. Lawrence (Himmelman and Hamel 1993). Barrie (1979) found Waved Whelks inhabiting a 4 to 90 m depth range in Nain, Labrador.

Life Cycle

Spawning and Fertilization: On the north shore of the Gulf of St. Lawrence, *B. undatum* typically copulates during late spring/early summer (May to July). There is often shoreward migration by this species prior to the copulatory behaviour (Martel *et al.* 1986a). Fertilization is internal and the female normally extrudes the fertilized eggs 2 to 3 weeks after copulation; however, a female is able to mate with more than one male and might store sperm for up to eight weeks before using it to fertilize her eggs.

Copulation by *B. undatum* in Swedish waters occurs around August (Valentinsson 2002) and between September and October in the Irish Sea (Kideys *et al.* 1993). Therefore, substantial temporal variability exists with respect to Waved Whelk reproduction at different locations. Difference in water temperature is likely a contributing factor to this variability.

Fertilized Eggs: The timing of fertilized egg deposition might extend as late as the end of August. The fertilized eggs of *B. undatum* are enclosed in benthic masses which may contain as many as 340,000 developing embryos. Preferred egg laying areas appear to be irregular surfaces, faces of boulders and kelp stalks. While attached to the substrate, the egg masses are vulnerable to predation by sea urchins and loss through detachment due to storm activity. There is no planktonic larval stage in this species, thereby limiting it's ability to disperse widely. The trochophore and veliger stages develop within the egg capsule (Fahy *et al.* 2000). In the northern Gulf of St. Lawrence, juveniles hatch after 5 to 8 months of embryonic development, generally during late autumn to late winter. Usually only 1% of the eggs successfully hatch. At hatching, the juvenile whelks are approximately 3 mm in shell length (Caddy *et al.* 1977; Martel *et al.* 1986a). Valentinsson (2002) reported that the principal egg-laying period for *B. undatum* in Swedish waters is probably between October and December.

Juveniles and Adults: Jalbert and Himmelman (1989) found that peak densities of particular size groups of *B. undatum* appear to be associated with specific habitats and depths in the northern Gulf of St. Lawrence. Their work indicated that as the Waved Whelks grew from recruitment size (< 1 cm) to immature adult size (3-7 cm), they moved from deeper sand-mud substrates to shallower, coarser substrates. Once they attained sexual maturity, the whelks returned to the deeper gravel/sand/mud areas (16 to 20 m depth). They concluded that this distributional shift might have been due to the distributions of the various sized prey of Waved Whelks. Himmelman (unpublished) has observed *B. undatum* individuals move 50 m over a two-day period. When not feeding or mating, juvenile and adult Waved Whelks typically spend much of their time immobile, either half buried in the sediment or on the surface of the substrate. The Waved Whelk appears to prefer habitats with moderate to high wave energies and moderate to strong currents (Himmelman 1988); however, they will exhibit substantial mobility in response to food and predators.

Golikov and Scarlato (1973) reported the summer and winter temperatures for the northern boundary of *B. undatum* distributional area as 5 °C and < 0 °C, respectively and the summer and winter temperatures for the southern boundary of its distributional area as 16 and 6 °C, respectively. The ranges of optimum temperatures of inhabitancy and spawning were given as 5 to 6 °C and 0 to 5 °C, respectively.

The lower lethal salinity limit is approximately 18 ppt (Staaland 1972). Drouin *et al.* (1985) reported that Waved Whelk abundance was much lower at their polyhaline sampling station (6 to 30 ppt) than at their station where the tidal salinities were more stable (24 to 30 ppt).

In the northern Gulf of St. Lawrence, Waved Whelks tend to grow slowly, but can reach lengths of 110 mm and ages of 15 years. Males mature at approximately 6 years (~ 70 mm) and females at 7 years (~ 75 mm) (Gendron 1992).

B. undatum is both a predacious and necrophagous carnivore, feeding primarily on molluscs and other invertebrates (Himmelman 1988). Himmelman and Hamel (1993) studied northern Gulf of St. Lawrence whelk diet in different habitats and different seasons. They identified this mollusc as one of the primary subtidal predators exploiting the bivalve and Sand Dollar resource in the northern Gulf. December collections revealed that the proportion of whelks with stomach

contents indicating feeding on sand habitat was significantly greater than those with stomach contents indicating feeding in rock, gravel and mud habitats, suggesting that more food resources were available for whelks on sandy bottoms. Urchins, polychaetes and amphipods were the most frequent prey items found in whelk stomachs from sandy areas. In whelks from rocky habitat, pieces of decapod crustaceans and fish eggs were the most common prey. Stomach contents from whelks collected in mud and gravel areas were essentially unidentifiable. These results confirmed that whelks are both active predators and carrion feeders. Feeding activity typically decreases sharply at the onset of breeding around late May (Martel *et al.* 1986b). Thompson (2002) investigated the circumstances under which whelks will attempt to feed on Blue Mussels. He found that whelks usually attempted to feed on mussels that had sustained tissue damage rather than healthy animals. Thompson (2002) felt that this supported the argument that the Waved Whelk is primarily a scavenger and has only limited success as a predator upon healthy bivalves. The Waved Whelk is one of the major predators in the more northern subtidal communities, whereas fish and decapod crustaceans are the predominant predators in more southern communities. *B. undatum* was one of the most abundant predators in the northern Gulf subtidal communities, generally occurring in the 0 to 5 m depth range.

Although lobsters are primary predators of the Waved Whelk, other predators include cod, crabs, sea stars and dogfish (Thomas and Himmelman 1988; Jalbert *et al.* 1989). Interestingly, Rochette *et al.* (1995; 2001) found that Waved Whelks inhabiting a location in the northern Gulf of St. Lawrence actually associated closely with one of their sea star predator species (*Leptasterias* sp.) in order to benefit from food resources (in this case, a surfclam species) made available by the sea star. Morissette and Himmelman (2000a) reported observations of *B. undatum* kleptoparasitizing *Leptasterias polaris*, especially when another sea star, *Asterias rubens,* was present. Brokordt *et al.* (2003) indicated that female *B. undatum* tend to be bolder in stealing food from the sea star, particularly just prior to egg laying. The risk associated with this is probably attenuated by the female whelk's greater capacity for escape responses compared to the male. Himmelman and Hamel (1993) also observed this interaction in the Gulf of St. Lawrence. The same type of association was observed in the Gulf of Maine between the Waved Whelk and another sea star species feeding on Horse Mussels (Fiorentino and Witman 1995).

Relation to Man

In the Gulf of St. Lawrence, Waved Whelks are harvested in a coastal fishery using pyramid-shaped traps deployed from small craft. Between 1987 and 1997, annual landings ranged from 400 to 1,300 mt in the Gulf of St. Lawrence. In 1998, exploratory licenses were issued to fishers in eastern Nova Scotia and Cape Breton (Kenchington and Glass 1998). Due to its sedentary life style, the Waved Whelk is quite vulnerable to over harvesting. Commercial catches of whelk around Newfoundland have been relatively poor in the past (Flight 1988). Kenchington and Lundy (1996) reported on a whelk test fishery in southwest Nova Scotia with a review of biological characteristics relevant to the development of the resource. Fahy *et al.* (2000) discussed various aspects of the Waved Whelk fishery in the southwest Irish Sea. Experimental whelk fishing was conducted in Conception Bay, Newfoundland in 1996 over a 10-day period. Slightly more than 1.5 mt were caught in depths ranging from 140 to 250 m (CAFID 1996).

The Waved Whelk has also been used as a bioindicator of chemical contamination (Svavarsson *et al.* 2001). Adult specimens were placed in various harbours at northern latitudes to assess the

bioavailability of organotins, particularly tributyltin. Bioavailability was determined by bioaccumulation and development of imposex.

3.3.3 Atlantic Jackknife Clam (*Ensis directus*)

General Distribution

The Atlantic Jackknife Clam (or Common Razor Clam) is distributed in the northwestern Atlantic Ocean from Labrador to Georgia. This bivalve may occur from the lower intertidal zone to a depth of 35 m in the subtidal zone. The preferred substrate for this deep-burrowing, often colonial clam is shifting sand (Gosner 1979), but it can also be found in mud and gravel. In eastern Canada, the identified subtidal clam beds are primarily in 5 to 8 m of water where currents are typically low to moderate (Kenchington *et al.* 1998).

Ensis directus was accidentally introduced into the North Sea in the late 1970s. Based on data collected from 1982 to 1994, Beukema and Dekker (1995) found that settlement in a Wadden Sea tidal flat area occurred in the summer over a wide range of intertidal levels. They observed that the highest survival rates for recruits were limited to areas below the level of mean low tides where the substrate was primarily composed of clean sands and there was only infrequent emersion. The population spread by 125 km per year to the north and by 75 km per year to the west against residual currents. This provides some insight into the possible spatial and temporal scales of larval dispersal (Armonies 2001).

Life Cycle

Studies on the biology of *E. directus* are few. Those that have been conducted provide some density information, a description of early developmental stages to 1.7 mm and some aging estimates (Sullivan 1948; Medcof 1958; Lambert 1994; Motnikar and Hotton 1995).

Spawning and Fertilization: The Jackknife Clam is dioecious. Kenchington *et al.* (1998) found that *E. directus* collected during mid-May had mature gametes even though water temperatures were less than 5 °C. Several of these clams commenced spawning within minutes of exposure to 20 °C seawater in the laboratory. Kenchington *et al.* (1998) reported that animals collected from a subtidal bed elsewhere in Nova Scotia were also spawning at this time. Eggs and sperm were released through excurrent siphons and fertilization occurred externally in the surrounding water.

Fertilized Eggs and Larvae: Within 24 hours of fertilization, the embryos had developed to the trochophore larval stage (Kenchington *et al.* 1998). After 11 days of development at 18 °C, the larvae had attained an average size of 186 x 215 µm. The larvae were fed phytoplankton during this time. The larvae reached pediveliger stage about 15 days after hatching, attaining an average size of 245 x 206 µm. At this point, the larvae were introduced to sand and they immediately burrowed into the substrate.

Juveniles and Adults: Armonies (1992) discussed the secondary dispersal of the Jackknife Clam spat after initial settlement. From the results of a study in a North Sea tidal flat from June to September, he concluded that the small spat (1 to 3 mm length) used byssus threads for drifting, while the larger juveniles (length greater than 3 mm) actively swam, primarily at night. He

observed that the peak abundances of juveniles re-entering the water column coincided with spring tides.

The juveniles reached lengths of 7 to 9 mm about 3 months after spawning (Kenchington *et al.* 1998). Small Jackknife Clams (< 20 mm) were absent from spring to fall sampling until September, indicating that these animals were from that year's year class. These small clams averaged 18 mm and ranged from 11 to 24 mm in length. One-year old clams were approximately 33 mm long. Lambert (1994) reported that two-year old Jackknife Clams in the North Sea were about 80 mm long and that after five years they had reached a length of 150 mm. The laboratory reared clams from a Nova Scotia stock attained a length of 80 mm after only 1.5 years (Kenchington *et al.* 1998). Kenchington *et al.* (1998) had collected a wide shell length range (10 to 160 mm) of Jackknife Clams from a Nova Scotia sand bar site with high exposure to wave energy. Although the distribution of Jackknife Clams at this location was patchy, all sizes of clams were found throughout the site.

E. directus has been identified as a key animal species of the biota assemblage associated with the "clam bed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. General physical characteristics typically associated with this type of habitat include fine to coarse sand/fine gravel substrate, full salinity and low to high exposure to wave energy (Hooper 1997). Examples of Jackknife Clam habitat in Newfoundland include Alexander Bay in Bonavista Bay, Shallow Bay in Gros Morne Park and The Tickle in Bonne Bay.

Colonies of *E. directus* are often associated with other bivalves such as softshell and surfclams (DFO 1996a). Kenchington *et al.* (1998) found that Jackknife Clams from the Nova Scotia sand bar were sharing this habitat with Atlantic Surfclams (*Spisula solidissima*). They are capable of burrowing to a depth of 25 cm in a few seconds. Various bird species that frequent intertidal flats have been reported feeding on *E. directus* (Schneider 1982; Swennen *et al.* 1985).

Relation to Man

For the most part, harvesting of this species is restricted to the use of hand held digging tools, although mechanical harvesters are used in certain areas such as the north shore of the St. Lawrence River in Quebec and at other Maritime locations where subtidal populations of this clam species have been found. Kenchington *et al.* (1998) suggested that a minimum commercial size of 120 mm (3 to 5 years old) be placed on Jackknife Clams in order to ensure that they spawn twice. The Jackknife Clam might be considered a feasible candidate for aquaculture given its fast growth and easily induced spawning (Kenchington *et al.* 1998).

3.3.4 Ocean Quahog (*Arctica islandica*)

General Distribution

The Ocean Quahog (Black Clam) is a bivalve mollusc found in temperate and boreal waters on both sides of the North Atlantic. This species occurs in the northwestern Atlantic Ocean from the Arctic to Cape Hatteras, North Carolina usually inhabiting the subtidal area at a depth range of 20 to 150 m. Ocean Quahogs have been found off Nova Scotia at depths less than 10 m (Caddy *et al.* 1974; Rowell *et al.* 1990; DFO 1998b) and are documented in areas deeper than

150 m. In Nova Scotia, the Ocean Quahog is most abundant in the inshore harbours and bays of southwestern Nova Scotia and the mouth of the Bay of Fundy and on the offshore banks, especially Sable and Western Banks, at ≤ 85 m depths (Rowell and Amaratunga 1986; DFO 1998b). Although *Arctica islandica* tends to prefer sand/mud bottoms, they also occur in lower densities on silt/clay or coarse sand/gravel substrates (Gosner 1979; Thompson *et al.* 1980; Fogarty 1981). Fogarty (1981) indicated that these molluscs occurred in highest densities in sediments containing high proportions of medium (0.25 to 0.49 mm) sand and shell fragments.

Life Cycle

Spawning and Fertilization: This dioecious species matures very slowly. In Nova Scotia, the age of sexual maturity for Ocean Quahog has been reported to be as high as 12 to 13 years (Duggan *et al.* 1998). In Iceland, the age of maturity for this clam species has been reported to be as old as 50 years. The environmental stimuli for spawning are unclear but probably include a combination of factors including bottom temperature, pH, food availability and dissolved oxygen levels.

Jones (1980; 1981) reported that over a two-year period, Ocean Quahogs collected off New Jersey exhibited gamete development between May (< 10% development) and August (100% development). It generally exhibits prolonged spawns from spring to summer, peaking later in the summer when water temperatures reach 15 °C (Ropes *et al.* 1981). Spawning commences when the bottom water temperature is about 13 °C. Off Nova Scotia, spawning has been reported from July to September (Rowell *et al.* 1990). Thórarinsdóttir and Steingrímsson (2000) indicated that spawning activity of Ocean Quahogs in Iceland waters appears to occur year round, but most intensely from June to August. Ocean Quahog larvae have been found as early as May off the U.S. east coast (Mann 1985), resulting from either spring spawning or late spawning the previous year. During the first year, partially spawned quahogs predominated in September and October before spawning out by late November. However, during the second year, partially spawned or spent individuals persisted into early February. These temporal differences between years may have been related to annual differences in water temperature. Fertilization occurs at water temperatures ranging from of 10 to 20 °C and is optimal at 15 °C (Landers 1976).

Fertilized Eggs and Larvae: The eggs of the Ocean Quahog are planktonic. Development of the fertilized egg is adversely affected at temperatures exceeding 20 °C (Landers 1976). Currents are principally responsible for egg dispersion (Ropes 1978).

Initially, trochophore larvae hatch from the fertilized eggs and these develop into veligers that in turn become pediveligers. Larvae are planktonic and may remain like this for as long as 8 weeks. Those raised at 13 °C metamorphosed in about 5 weeks, while those raised at 9 °C did not metamorphose until the eighth week after hatching (Mann 1979). Mann and Wolfe (1983) proposed 6 °C as the minimum water temperature at which Ocean Quahog larvae develop relatively well.

Mann (1985) found that bivalve larvae on the southern New England shelf were most abundant during late August and September at depths greater than 10 m, water temperatures of 14 to 18 °C

and chlorophyll *a* concentrations of < 2 µg/l. In October, the larvae were most abundant in surface water at temperatures of 15.5 °C and chlorophyll *a* concentrations of about 3.0 µg/l. Ocean Quahog larvae, along with larvae of Horse Mussels and Atlantic Surfclams, dominated the proportion of larvae greater than 200 µm in length. *A. islandica* settle in waters off North Iceland mainly in August and into the September to November period (Garcia *et al.* 2003). Ocean Quahog larvae are planktotrophic, feeding primarily on unicellular algae (Cargnelli *et al.* 1999a).

Juveniles and Adults: Ocean Quahogs are very long-lived (100+ years), shallow burrowers that tend to reach sizes of about 130 mm. Individuals as old as 202 years have been collected in Icelandic waters (Steingrímsson and Thórarinsdóttir 1995). Growth tends to slow after about 15 years of age (Thompson *et al.* 1980). Mann (1990) suggested that Ocean Quahogs are rather sedentary and that larval settlement determines adult distribution rather than immigration of post-settlement stages. Golikov and Scarlato (1973) reported that the optimum temperature range for inhabitancy was 6 to 16 °C. The Ocean Quahog is able to survive and grow in areas where water currents are low (Kerswill 1949). Optimal salinity has been documented as 31 to 33 ppt. Kraus *et al.* (1991) demonstrated the tolerance of adult Ocean Quahogs at salinities ranging from 15 to 30 ppt at two temperatures, 6 and 19 °C.

Witbaard *et al.* (1997) reported on laboratory experimentation that investigated the effects of water temperature on the growth of juvenile Ocean Quahogs. *A. islandica* was able to continue its growth at temperatures as low as 1 °C. Between 1 and 12 °C, the quahog displayed a tenfold change in growth rate, the greatest change occurring between 1 and 6 °C. Witbaard *et al.* (1999) concluded that while shell growth was positively correlated with water temperature, it was inversely correlated with depth and silt content of the sediment. Some of their North Sea specimens had strong positive correlation with sediment grain size, probably because areas with coarser substrate also had more bottom current and therefore, more lateral seston flux which translated into additional food supply.

The highest densities of *A. islandica* found during winter and spring surveys off Iceland were at depths ranging from 15 to 30 m and on substrates consisting primarily of silt and fine sand (Thórarinsdóttir and Einarsson 1996). Ocean Quahog abundance dropped drastically on gravel substrate. Although Thórarinsdóttir (1997) did not find any significant depth effect on Ocean Quahog abundance in an Icelandic fjord, densities were highest in sediments with high proportions of medium-grained sand. Juveniles were more widely distributed than the adults, perhaps to lessen predation effect. The juvenile Ocean Quahogs were found at depths ranging from 6 to 40 m and were most abundant between 17 and 34 m. Duggan *et al.* (1998) surveyed stocks in the Bay of Fundy at depths of 32 to 49 m and on substrates comprised primarily of sand with patches of clay. Ocean Quahogs were most abundant on the southern flank of Georges Bank at a depth range of 60 to 75 m (Lewis *et al.* 2001). The results suggest that recruitment of small Ocean Quahogs on Georges Bank has been highly variable during the last 40 years (Lewis *et al.* 2001).

In areas of the western Baltic Sea, the Ocean Quahog is considered the most important species occurring below the halocline (Zettler *et al.* 2001). Juveniles dominated the distribution at a depth range of 15 to 20 m, while adults were dominant at 20 to 25 m. This bivalve species has

been identified as a key animal species in the biota assemblage associated with "clam bed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. General physical characteristics typically associated with this type of habitat include fine to coarse sand/fine gravel substrate, full salinity and low to high exposure to wave energy (Hooper 1997). Examples of Ocean Quahog habitat in Newfoundland include Alexander Bay in Bonavista Bay, Shallow Bay in Gros Morne Park and The Tickle in Bonne Bay.

The juvenile and adult quahogs are suspension feeders on phytoplankton, using their siphons to pump in water from which to feed. Witbaard *et al.* (2003) suggested that the shell growth of *A. islandica* in the North Sea is influenced negatively mainly by the abundance of copepods. During years of dense copepod production, a major portion of the downward flux of food particles is intercepted by the copepods, thereby depriving the bivalves of food. The numerous predators of the Ocean Quahog include Rock Crab, sea stars, Hermit Crab, Moon Snails, whelks and numerous groundfish species (cod, flounder, sculpin, Ocean Pout) (Cargnelli *et al.* 1999a). In some areas, the American Lobster (*Homarus americanus*) is the primary predator of the Ocean Quahog (Beal and Kraus 1991).

Relation to Man

Brey *et al.* (1990) discussed the importance of *A. islandica* to the cod population in a bay of the western Baltic Sea. They estimated that the Ocean Quahogs in this area were responsible for at least 40% of cod production.

The Ocean Quahog has had considerable commercial value off the east coast of the U.S., but fishing pressure on this species reduced the catch per unit effort (CPUE) off New Jersey by 29 % from 1986 to 1992 (Kennish *et al.* 1994).

Kraus *et al.* (1990; 1992) compared growth rates of wild and laboratory reared Ocean Quahogs and their results indicated potential for this species to be successfully cultivated in food rich, shallow water sites protected from predators.

3.3.5 Atlantic Surfclam (*Spisula solidissima*)

Distribution

The Atlantic Surfclam (Bar Clam) inhabits sandy northwest Atlantic Ocean continental shelf habitats from the southern Gulf of St. Lawrence to Cape Hatteras, North Carolina (DFO 1996a; 1996b; Cargnelli *et al.* 1999b). According to Gosner (1979), its range extends northward to Labrador. Individuals commonly occur from the shallow subtidal zone to depths of 50 m (Weinberg and Helser 1996).

Life Cycle

Spawning and Fertilization: This dioecious bivalve typically spawns in the summer and early fall, commencing and ending earlier in the southern part of its range. Unfertilized Atlantic Surfclam eggs are about 56 µm in diameter, unpigmented and relatively yolk-free. These are characteristics often associated with planktotrophic eggs. Spawning typically occurs once water temperatures reach 12 to 15 °C (DFO 1996a) and there is sometimes a second, minor spawning

event in the fall caused by the breakdown of the thermocline. Fertilization occurs in the water column above the beds of spawning clams and is optimal at 6 to 24 °C, salinities of 20 to 35 ppt and a pH of 7.8 to 10 (Fay *et al.* 1983).

Sephton (1987) examined the reproductive cycle of the Atlantic Surfclam around Prince Edward Island over two years between April and December. He found that gametogenesis was complete by June-July as water temperatures approached 15 °C and prolonged spawning occurred during the warm water period of late July to October. Spawning ended abruptly as water temperatures fell in October.

Jones (1980; 1981) reported that over a two-year period, Atlantic Surfclams collected off New Jersey exhibited complete gamete development by late May or June. The percentage of partially spawned individuals increased sharply in late summer months and by November-December, 100% of the clams appeared spent (i.e. spawned out).

Fertilized Eggs and Larvae: Walker and O'Beirn (1996) reared *Spisula solidissima* through the embryonic and early larval development period under laboratory conditions. The water temperatures remained within the 20 to 22 °C range and salinity was maintained at 25 ppt. Relative to fertilization time, they observed the ciliated blastula at 6 hours, the trochophore larvae at 17 hours and an active probing foot by the eighth day (immediate pre-settlement).

Pyramid-shaped trochophore planktonic larvae hatch approximately 9 hours after fertilization at 22 °C and after 40 hours at 14 °C. Veliger larvae appear in 72 hours at 14 °C and in 28 hours at 22 °C. The pediveliger larvae occur about 18 days after fertilization at 22 °C. Metamorphosis to the juvenile stage and subsequent settlement to the substrate occur approximately 19 to 35 days after fertilization, depending on water temperature. Weissberger (1998) reported larval settlement off New Jersey in late June and early July, followed by a smaller settlement pulse in December. Larval size at metamorphosis is about 250 µm.

Larvae tolerate temperatures of 14 to 30 °C and develop optimally at 22 °C. They are capable of growth in salinities as low as 16 ppt and can survive in salinities of 8 ppt as long as temperatures are low. In the field, high Atlantic Surfclam larval concentrations have been found in water masses with water temperatures of 14 to 18 °C. In New Jersey, high concentrations of Atlantic Surfclam larvae have been found in the spring (derived from inshore clams) and fall (derived from offshore clams) (Tarnowski 1981). Dispersal by currents occurs during the larval stage and settlement may coincide with the relaxation of upwelling events.

Mann (1985) discussed the seasonal change in occurrence, depth distribution, size distribution and species composition of bivalve larvae, including *S. solidissima*, at a single station on the southern New England shelf between April and December. These data were related to water temperatures and chlorophyll *a* conditions. Atlantic Surfclam larvae were most abundant during late August and September at depths greater than 10 m, water temperatures of 14 to 18 °C and chlorophyll *a* concentrations of < 2 µg/l. In October, the highest larval concentration was found at the surface at a temperature of 15.5 °C and chlorophyll *a* concentrations of approximately 3.0 µg/l. Atlantic Surfclam larvae were one of three species that dominated larvae greater than 200

μm in length. Atlantic Surfclam larvae were present from late July to October and extended into shallower, warmer waters than the larvae of Horse Mussels and Ocean Quahogs.

Snelgrove *et al.* (1998; 1999a) conducted laboratory experiments which indicated larval habitat selection contributed to sediment-specific (sand rather than mud) adult Atlantic Surfclam field distributions. Snelgrove *et al.* (2001) conducted field experiments to determine whether pattern and diversity in benthic sedimentary communities are set primarily at colonization or by post-settlement biological interactions. They conducted reciprocal sediment transplant experiments at both a sandy and a muddy site in Newfoundland waters at a depth of 12 m. *S. solidissima* was a dominant species at the sandy site. They found that species patterns in some environments may be set through habitat selection by larvae and juvenile colonization from the surrounding community. MacKenzie *et al.* (1984) showed that pediveliger prefer coarse sand over fine sand or mud when settling to the bottom.

Weissberger and Grassle (2003) conducted a long-term study (1993-1996) of factors affecting inshore recruitment of surfclams at 12 m deep sites off New Jersey. Part of the study considered settlement by *S. solidissima.* They found that a large pulse of surfclam settlement occurred during the late June-early July period in all four years and that there was some low-level settlement as late as December in some years. The settlement appeared to be correlated with down welling following nearshore upwelling events.

Juveniles and Adults: The greatest concentrations of Atlantic Surfclams are typically found in well sorted, medium sand, but they also occur in fine sand and silt/fine sand. They are most common at depths of 8 to 66 m in turbulent areas (i.e., moderate to full exposure to wave energy and moderate to strong currents) (Cargnelli *et al.* 1999b) below the breaker (or surf) zone and in areas where bottom temperatures rarely exceed 25 °C. Minimum temperatures experienced by these clams are probably not less than 1 °C. Atlantic Surfclams are normally found at salinities exceeding 28 ppt. Surfclams are able to reach sexual maturity as early as 3 months after settlement (New Jersey) (Chintala and Grassle 1995) or as old as 4 years (Prince Edward Island). There have been reports of surfclams as old as 31 years and as large as 226 mm (Robert 1981).

A stock assessment in Prince Edward Island (Robert 1981) indicated three zones of bar clam abundance within an approximately 200 m wide band along coastal flats. The 100 m wide nearshore zone within the intertidal zone contained primarily pre-recruit Atlantic Surfclams (40 to 50 mm shell width). The frontal zone at the extreme low water mark was about 50 to 75 m wide and contained 80% recruit-sized clams. The 25 to 50 m zone below the frontal zone was subtidal and it contained very few Atlantic Surfclams. The distribution of *S. solidissima* commonly overlaps with that of the Atlantic Jackknife Clam (*Ensis directus*) (DFO 1996a).

Meyer *et al.* (1987) monitored a benthic infaunal community dominated by the Atlantic Surfclam near Long Island, New York. They found that larger surfclams (104-138 mm shell length) burrowed to a depth of 12 to 14 cm, while the smaller ones (26-62 mm shell length) burrowed to 2 to 4 cm below the sediment surface. The study area was characterized by high substrate mobility, with fine to medium sands inshore and silty-fine sands offshore. Annual bottom temperatures ranged from 5 °C in winter to 20 °C in the summer and salinities ranged from 30 to 33 ppt.

Weissberger and Grassle (2003) found that surfclam growth rates off New Jersey between 1993 and 1996 varied during the summer and between years, probably reflecting low and high bottom temperatures during nearshore upwelling and down welling events, respectively. Growth during the winter months was negligible. The authors concluded that inshore surfclam growth rate is temperature dependent and that survival to one year is dependent on high-density settlement in the preceding summer. In addition to concurring that the down welling and upwelling hydrodynamic events effect larval supply, Chintala and Grassle (2001) also concluded that cool bottom temperatures probably reduce predator impacts on the recently settled surfclams.

A study by Cerrato and Keith (1992) confirmed a trend of reduced adult growth, maximum size and lifespan for Atlantic Surfclams observed in inshore versus offshore Atlantic Ocean stocks. They showed an extended shoreward range for this species, but the results clearly indicated that its distribution into estuarine habitats is fundamentally limited by physiological constraints imposed by the temperature and salinity regime rather than by biotic interactions.

Atlantic Surfclams are planktivorous suspension feeders. Diatoms and ciliates have often been identified in surfclam guts. Suspended clay particles may inhibit feeding by this species. Surfclams have numerous predators including snails, sea stars, crabs, haddock and cod. Tsipoura and Burger (1999) reported that during a severe storm along the Atlantic shore of New Jersey, a large number of surfclams were washed onto the beach. Subsequently, thirty-nine shorebirds (*Calidris alpina*) were found with their bills caught between the two valves of the clams. It is likely that *S. solidissima* may be an important prey item.

Relation to Man

Since the 1960s, the Atlantic Surfclam has supported a major fishery on the U.S. northeastern continental shelf (Yancey and Welch 1968). The number of year classes in the most heavily exploited populations increased between 1978 and 1997 after these populations were found to be at historical lows in the mid-1970s (Weinberg 1999).

This species is being investigated as a potential aquaculture species in numerous locations, including Canada. Walker (2001) reared *S. solidissima* in field culture to determine the effects of stocking densities on clams cultured in bottom cages and mesh bags, bottom cage versus mesh bag culture and bag mesh size on growth and survival of surfclams in coastal Georgia. He determined that 1)mean clam size tended to decrease with increases in stocking densities; 2) surfclams had greater growth and survival rates with greater production in bottom cages compared to mesh bags and 3) smaller mesh size increased mortality.

3.3.6 Arctic (Stimpson's) Surfclam (*Mactromeris polynyma*)

Distribution

The Arctic Surfclam, a circumboreal species, inhabits both the Atlantic and Pacific Oceans. It is the largest clam in the northwestern Atlantic Ocean and occurs from Labrador to Rhode Island often on medium to coarse sand substrate (Abbott 1974). In the Canadian part of its range, this species occurs in commercial quantities in the offshore areas of the Scotian Shelf and Eastern Grand Banks and in inshore areas off southwest Nova Scotia and in the Gulf of St. Lawrence (DFO 1989a; 1999; 2004a).

Life Cycle

Spawning and Fertilization: Arctic Surfclams are dioecious and typically reach reproductive maturity at 5 to 8 years of age. Spawning generally occurs during the fall, although there is indication that some inshore populations may also exhibit spring spawning (DFO 1999).

Fertilized Eggs and Larvae: Davis and Shumway (1996) found under laboratory conditions that *Mactromeris polynyma* larvae hatched one day after spawning at 15 °C and four days after spawning at 8.5 °C. In the same study, metamorphosis to the post-larval stage occurred in 24 days at 15 °C and in 42 days at 10 °C.

Juveniles and Adults: The Arctic Surfclam is a long-lived, sedentary, slow growing infaunal species. There is a general lack of biological information on this species. They appear to prefer substrates comprised primarily of medium to coarse sand into which they are able to burrow (DFO 1999). Davis and Shumway (1996) reported that the growth rate of this bivalve was greatest in silt/sand substrates. Caddy *et al.* (1974) indicated that this surfclam species buries itself a little deeper in the sediments than does the Atlantic Surfclam (*S. solidissima*).

Exploratory surveys conducted on Banquereau Bank (eastern Scotian Shelf) between 1980 and 1983 collected Arctic Surfclams ranging in shell length from 24 mm to 157 mm (Amaratunga and Rowell 1988). Samples collected on Banquereau Bank (depths 50 to 100 m) in 1996 and 1997 contained individuals with shell lengths as large as 140 mm and as old as 60 years (Roddick and Smith 1999). Based on the locations of these sample collections, this bivalve prefers habitats with high salinity (> 18 ppt) and lower water temperatures. Recruitment for this on Banquereau Bank species has been estimated at age 20 (Roddick *et al.* 2007).

Diver and dredge sampling for Arctic Surfclams in the northern Gulf of St. Lawrence during 1993 and 1994 revealed information regarding other species comprising the benthic community. The Arctic Surfclams dominated the community, but other abundant benthic species included whelks (*Buccinum* sp.), Arctic Wedge Clam (*Mesodesma arctatum*), Greenland Cockle (*Serripes groenlandicus*), truncated Softshell Clam (*Mya truncata*) and Northern Propeller Clam (*Cyrtodaria siliqua*). Sand Dollars, brittle stars, Green Sea Urchins and juvenile Snow Crab were also observed at some of the stations (Lambert and Goudreau 1996). Sampling tows were conducted on mud and/or sand substrate over a depth range of 13 to 25 m and samples were collected from the upper 15 cm of substrate. Hughes and Bourne (1981) found that the densest aggregations of *M. polynyma* at their study area in the Bering Sea occurred at about 30 m depth and at a salinity range of 29 to 32 ppt. Iceland Scallops in the northern Gulf of St. Lawrence were observed using empty *M. polynyma* shells as refuges (Arsenault and Himmelman 1998a).

Arctic Surfclams are filter feeders with a microalgal diet (e.g., dinoflagellates). Smith and Wikfors (1992) investigated this clam for the presence of phytoplankton pigments in selected tissues. Rochette *et al.* (1995) and Himmelman and Hamel (1993) observed the predation on the Arctic Surfclam by the sea star *Leptasterias polaris* in the northern Gulf of St. Lawrence. The Waved Whelk (*Buccinum undatum*) would attempt to scavenge meat from the surfclam, despite the presence of the sea star that also predates on whelks. Morissette and Himmelman (2000a) indicated that other kleptoparasites, including sea stars (*Asterias rubens*), Rock Crab (*Cancer*

irroratus) and Lyre Crab (*Hyas araneus*) fed on the Arctic Surfclam as well. Large groundfish are also primary predators of this surfclam species. Roddick and Lemon (1992) found that Atlantic Cod on Banquereau Bank were feeding on *M. polynyma*. This clam species has also been documented as a principal prey item for sea otters in Alaska (Green and Brueggeman 1991).

Relation to Man

In the late 1980s, a directed fishery for this surfclam began in response to the opening of a high value sushi and sashimi market in Japan (Roddick and Kenchington 1990). Surveys and test fisheries on the Scotian Shelf were conducted during the 1980s to determine distribution, abundance and estimates of commercially harvestable biomass of this species (Amaratunga and Rowell 1986; Rowell and Amaratunga 1986). On the Banquereau Bank off southeastern Nova Scotia, the fishery for this surfclam grew from 1986 landings of 29 mt to just under 25,000 mt in 1998. A fishery for the Arctic Surfclam has occurred on the Grand Banks since 1989 (Roddick and Smith 1999). The present fishery for this species is conducted using large freezer processors with hydraulic dredges and clams in the 10 to 15 year age range are targeted (DFO 1999). In the Gulf of St. Lawrence, Arctic Surfclam fishing is a relatively recent activity. The most viable commercial beds in the Gulf are located on Quebec's North Shore and in the Îles-de-la-Madelaine area. The long-term future of this fishery remains unclear. However, there are indications that *M. polynyma* may be amenable to aquaculture in Maine and the Maritimes (Davis and Shumway 1996; Davis 1999).

Results of a study conducted by Fournier *et al.* (2002) support the use of *M. polynyma* as a sentinel species to monitor sediment contamination. The study used hemocyte phagocytic activity as the biomarker of exposure to organic contaminants in marine sediments collected in Quebec, Canada. Sauve *et al.* (2002) and Bouchard *et al.* (1999) also conducted a study of phagocytic activity of marine bivalves in response to exposure of haemocytes to various metal contaminants and butyltin compounds, respectively.

3.3.7 Softshell Clam (*Mya arenaria*)

General Distribution

The Softshell Clam is widely distributed in both North American and European coastal waters. In the northwestern Atlantic Ocean, this bivalve occurs primarily from Labrador south to Cape Hatteras, with lower abundances as far south as Florida (Strasser 1998). Adults have an aggregated distribution and are normally limited to intertidal and shallow subtidal zones in soft bottom estuarine areas; however, they have occurred at depths as great as 200 m (Newell and Hidu 1986). The Softshell Clam occurs in small, localized beds around Newfoundland (DFO 1989a; DFO 1996c). Examples of Softshell Clam bed locations in Newfoundland include Piccadilly in Port au Port Bay, St. Paul's Harbour, Stephenville Crossing in St. George's Bay and Salmonier (Hooper 1997). Barrie (1979) found Softshell Clam in sandy substrates at various Labrador locations and in Conception Bay, Newfoundland over a depth range of 3 to 60 m.

Life Cycle

Spawning and Fertilization: Clams with a shell length exceeding 20 mm (2 or 3 years old) are generally capable of spawning. Gametogenesis typically commences in late winter-early spring (Newell and Hidu 1986). It has been suggested that exposure of Softshell Clams to anti-estrogenic contaminants has the potential to delay gametogenesis (Gauthier-Clerc *et al.* 2002). Depending on water temperature and food availability, the dioecious Softshell Clam spawns sometime during the June to September period, usually peaking around July when water temperatures reach approximately 20 °C. Initiation of spawning occurs once water temperatures are approximately 10 to 12 °C (Caddy *et al.* 1977). In some cases (south of Cape Cod), an additional spawning event may occur in early to late fall (Brousseau 1978). Males generally spawn before the females. Fertilization is external after gamete release through the excurrent siphon (DFO 1993a). Female fecundity increases with individual size. Females of shell length 63 mm have been shown to be capable of releasing as many as 3 million eggs per year, but there is considerable variation.

Fertilized Eggs and Larvae: The gelatinous fertilized eggs (~ 66 µm in diameter) are benthic and persist for up to 12 hours before hatching occurs. Hatched larvae (trochophore and veliger stages) remain planktonic for 2 to 3 weeks prior to settlement and can be carried substantial distances from their hatching location. The optimal water temperature range for larval development is about 17 to 23 °C, although slow development can occur at temperatures as low as 10 °C. The larvae are less tolerant to salinity fluctuation than the adults and appear to prefer a range of 16 to 32 ppt (Stickney 1964). Along the New Hampshire coast, Softshell Clam larval abundance peaked in late summer and was higher in inshore waters than offshore waters. Larval density was greater at water depths of 5 to 9 m as compared to surface waters and at 13 m depth (Newell and Hidu 1986).

Roegner (2000) discussed the transport of molluscan larvae through a shallow estuary in Nova Scotia. He concluded that in certain estuarine systems, tidal flow is too substantial for larvae not to be exported from the hatching area to the coastal ocean. This means that the temporal persistence of bivalve populations, such as the Softshell Clam, in such estuaries is probably dependent on larval invasion. It is most likely that many estuaries in an area contribute to a larval pool residing in the nearshore zone and feeding the estuaries under appropriate oceanographic conditions.

The larvae feed on microplanktonic organisms in the water column and, in turn are susceptible to predation by other planktivores. Raby *et al.* (1997) investigated food particle size and selection by bivalve larvae, including Softshell Clam veligers, in the Baie des Chaleurs, Gulf of St. Lawrence. The September sampling was conducted 2 to 14 m below the surface at a 20 m depth location approximately 3 km offshore. The water column was well mixed from top to bottom. Blue Mussels and Softshell Clams dominated this veliger community which also included Sea Scallop larvae. They found that Softshell Clam veligers (185 to 260 µm) fed less on < 5 µm and 5 to 15 µm algal cells than did the mussel and Sea Scallop larvae. The larger softshell larvae (261 to 405 µm) contained more < 5 µm cells than the mussels.

Burke and Mann (1974) studied a shallow estuary in Nova Scotia between April and November. They found that Softshell Clams commenced settlement to the sand flat bottom in August and continued until November. Upon settlement, larvae metamorphose into juvenile spat. Snelgrove *et al.* (1999b) investigated the differences between degrees of settlement at two Nova Scotian intertidal locations approximately 300 m apart, one sheltered and the other exposed. Results indicated higher settlement by the *Mya arenaria* larvae onto the finer sediments from the sheltered location. Emerson and Grant (1991) observed significantly more Softshell Clam spat at an exposed site as compared to a sheltered one. It is obvious that both pre- and post-settlement processes determine the adult Softshell Clam distribution at these locations.

A study conducted in New Brunswick focused on Softshell Clam spat settlement on various artificial substrates (Chandler *et al.* 2001). Results indicated that collectors which accumulated sediment within their structure also collected more spat than those which did not accumulate sediment. The study also indicated that spat collection was maximized at the mid-intertidal area and that settlement was reduced when the collectors were fouled with intertidal green algae.

Juveniles and Adults: Spat may remain in a floating/crawling mode for 2 to 5 weeks, attaching to the substrate (eelgrass, filamentous algae, abiotic substrate) with byssal threads. As they grow larger, the spat begin to burrow into the soft sediment, with burrowing depth increasing with age and size. Once these animals reach a shell length of approximately 5 mm, they are referred to as "seed clams". Juvenile seed clams may migrate shoreward as far as several hundred meters.

Although growth is slowest in the upper intertidal zone, survival is highest . Optimal growth occurs in fine sediments (sand or sandy mud) in the lower intertidal zone where food availability is greatest. Faster water currents tend to support greater population densities. This species has been found as deep as 200 m. Since the adults live in permanent burrows, shifting sand habitat is not appropriate because of the potential of suffocation. Thiel *et al.* (1998) indicated potential lethal effects of green algal mats on this clam by acting as a barrier to siphon extension. Burrowing is difficult in sand with grain sizes exceeding 0.5 mm diameter. Newell and Hidu (1982) demonstrated the effects of sediment type on the growth of the Softshell Clam. Clam growth was more rapid in fine sediments (mud/sand) than in coarse sediment (gravel). Clams grown in sand were longer and narrower than those grown in mud, while those grown in gravel were more globose than any of the others. Appeldoorn (1982) observed a distinct latitudinal growth relationship, with Softshell Clam growth decreasing towards the north. Temperature, tidal height, tidal position and substrate conditions systematically varied with latitude, with temperature appearing to be the dominant factor affecting growth.

Brousseau and Baglivo (1988) compared two populations of *M. arenaria* in Long Island Sound, living in slightly different substrates. They found that those clams inhabiting the larger grained sediment had lower growth rates, lower egg production and lower survival rates. The difference could be due to the higher maintenance demands in the coarser substrate from burrowing and valve activity.

Overall, Softshell Clams have wide tolerances to fluctuations in salinity and water temperature (euryhaline and eurythermal, respectively). Preferred salinity levels appear to decrease moving south through the distribution area. The lowest salinity tolerance observed for this species is

about 5 ppt, while the optimum is between 25 to 35 ppt. Salinity tolerance of the Softshell Clam appears to be linked to water temperature. Generally, the preferred temperature range of this clam is 6 to 14 °C, but it can withstand freezing for up to 7 weeks (Caddy *et al.* 1977). Bourget (1983) reported on seasonal variations of cold tolerance in *M. arenaria* in the St. Lawrence Estuary. Median lethal temperatures for this species ranged from –10 to –15 °C, with juvenile Softshell Clams showing less cold tolerance than large ones. Softshell Clams can cope with increased turbidity to a point by reducing ventilation rate, but if this behaviour is sustained, starvation will occur (Grant and Thorpe 1991).

Beukema *et al.* (2001) studied *M. arenaria* in the Wadden Sea, Netherlands. Based on data collected from 1973 to 1999, they noticed that recruitment (0-group density) was noticeably higher following colder than normal winters. Hypothesized reasons for this included 1) lower weight loss at lower water temperatures resulted in higher adult weights and conditioning and subsequently, better egg production; 2) lower abundance of predators in the spring due to the harsh winter and 3) higher competitor mortality over the winter resulted in less competition for the infaunal clams.

These filter feeders ingest flagellates, diatoms, bacteria, organic detritus and dissolved organic molecules. Since these clams burrow as deep as 30 cm, they use a siphon to pump seawater from above the substrate in order to feed and respire. Softshell Clams are most vulnerable to predation during larval, spat and early juvenile stages. Predators on larvae include zooplankton, fish and various filtering invertebrates. Softshell Clam spat and early juveniles are prey to gastropods, polychaetes, shrimp, echinoderms, fish (rays, flounder, cod and sculpin) and various birds (ducks, cormorants, gulls, crows). Stehlik and Meise (2000) and Phelan *et al.* (2001) discussed the obvious prey preference shown by Winter Flounder for *M. arenaria*. Skilleter (1994) described an estuarine bivalve association in North Carolina that may represent an example of associational defence. He observed that Softshell Clams sharing habitat with potentially competing bivalves were less prone to predation by crabs, perhaps because of the greater amounts of time the crabs spent handling non-food items. Nemerteans are important predators of newly settled larvae in marine soft bottom communities, especially in the intertidal areas (Ambrose 1991; Bourque *et al.* 2001a; b). Bourque *et al.* (2002) described the searching and feeding behaviours of a common Atlantic Canada nemertean, *Cerebratulus lacteus*, a known predator of *M. arenaria*. The invasive green crab (*Carcinus maenas*) has also been identified as an important predator of *M. arenaria* in Atlantic Canada (Floyd and Williams 2004).

The Softshell Clam has been identified as a key animal species of the biotic assemblage associated with "clam bed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. General physical characteristics typically associated with this type of habitat include fine to coarse sand/fine gravel substrate, full salinity and low to high exposure to wave energy (Hooper 1997). Densities of clams tend to be highest in eddies, along the sides of sand bars or islands, at mouths of rivers/streams emptying into shallow estuaries and in slack water adjacent to swift current. Dunn *et al.* (1999) presented results which suggested that biological disturbance such as those imposed by the activities of mobile benthic deposit feeders might play an important role in post-larval transport and subsequent distribution. They surmised that the biological disturbances could resuspend the post-larvae and then bottom currents would redistribute them.

Relation to Man

Softshell Clams may reach harvestable size within one to two years of settlement. Approximately 70 mt of Softshell Clams were harvested during an experimental fishery conducted near Burgeo, Newfoundland in 1994 (DFO 1996c). Commercial fisheries for this species are much more substantial in other areas of eastern North America. The Softshell Clam has been considered as a candidate for aquaculture in the Canadian Atlantic provinces and northeastern U.S. states.

The Softshell Clam has also been used as a bioindicator species in numerous environmental effects monitoring programs (Pellerin-Massicotte 1994; Meade *et al.* 2000; Blaise *et al.* 2002). There is some evidence that *M. arenaria* exposed to elevated levels of tributyltin are subject to masculinising effects or imposex, as is the case with some other marine invertebrates (Gagne *et al.* 2003). Hamoutene *et al.* (2002) did not find any significant effects of copper mine tailings on the biochemical or histological properties of Softshell Clams at a Newfoundland location.

3.3.8 Cockles (*Serripes groenlandicus; Clinocardium ciliatum*)

Serripes groenlandicus (Greenland (Smooth) Cockle): The Greenland Cockle is widely distributed throughout the Arctic Ocean and southward in varying degrees (Golikov and Scarlato 1973). In the northwest Atlantic Ocean, this bivalve is found from Greenland to Cape Cod at subtidal depths $\geq$ 9 m. Barrie (1979) found this cockle species on sandy substrates within a depth range of 6 to 18 m at various Labrador locations. It is approximately 100 mm in diameter at full growth (Gosner 1979). The life history of the Greenland Cockle is poorly understood.

Garcia *et al.* (2003) investigated the seasonal pattern of bivalve spat settlement in North Iceland using artificial collectors over a 14-month period. Their results indicated that *Serripes groenlandicus* settled primarily in August and September when mean water temperatures were > 8 °C. Collectors at 5, 10 and 15 m had equal abundances of Greenland Cockle spat.

Golikov and Scarlato (1973) reported temperatures for the northern boundary of its distributional area of $\leq$ –0.4 °C and summer and winter temperatures for the southern boundary of its distributional area of 12 °C and 8 °C, respectively. The ranges of optimum temperatures of inhabitancy and spawning were given as –0.4 to 8 °C and 0 to 10 °C, respectively.

Jørgensen *et al.* (1999) examined macrobenthic faunal associations, hydrography and sediment structure at 14 stations in the Kara Sea (Arctic Russia). *S. groenlandicus* was the most conspicuous species at three of the stations. One of the stations had substrate that was 63% mud (< 63 µm), while the sediments at the other two stations were only 8% mud. The water temperature at the muddier station was –0.62 °C and 0.29 to 0.47 °C at the other two stations. Depths (23 to 24 m) and salinities (34.13 to 34.21 ppt) at all three stations with Greenland Cockles were essentially the same.

The Greenland Cockle rarely burrows more than 7 cm from the substrate surface and therefore must rely on its escape behaviour to limit predation. This cockle displayed its most intense escape behaviour towards the sea stars *Leptasterias polaris* and *Asterias rubens,* two of its primary predators (Legault and Himmelman 1993). Other predators of *S. groenlandicus* include

demersal fish (e.g., cod, haddock) (Dolgov and Yaragina 1990) and marine mammals (Fisher and Stewart 1997; Born *et al.* 2003).

Clinocardium ciliatum (Iceland Cockle): In the northwestern Atlantic Ocean, the Iceland Cockle generally occurs from Greenland to Massachusetts at subtidal depths of 6 m or more. It is approximately 50 mm in diameter at full growth (Gosner 1979). Its life history characteristics are not well known. Gilbert *et al.* (1984) reported finding juvenile Iceland Cockles in mud/sand substrates in the shallow subtidal (~ 29 m) below the intertidal flats near Nain, Labrador. Barrie (1979) found this cockle species on sandy substrates at various Labrador locations over a depth range of 6 to 62 m. Prena *et al.* (1999) reported that this species was one of four dominant mollusc species found during otter trawling on a fine to medium grained sandy bottom ecosystem on the Grand Banks of Newfoundland. The depth range of the study area was 120 to 146 m. The sampling sled collected epibenthos and infauna in the upper 3 cm of the substrate. Gilkinson *et al.* (1998) indicated that the large near-surface bivalves such as the Iceland Cockle occurred in lower densities than smaller bivalves in the sandy area on the Grand Banks.

The annual growth of *Clinocardium ciliatum* at three different sites in the Norwegian Arctic was studied by Tallqvist and Sundet (2000). The depth, substrate and influencing water mass characteristics of each site were as follows: (1) 80-118 m with a mainly clay substrate and cold Arctic water; (2) 112-130 m with a mainly gravel substrate with clay patches and Atlantic water; and (3) 100-130 m with a mainly clay substrate and Atlantic and Arctic water. The three sites were also at different latitudes. The study indicated that higher Arctic latitudes and Arctic water masses did not reduce the growth of *C. ciliatum* compared to the most southern site. Iceland Cockles at the site with only Arctic water influence exhibited the highest annual growth, indicating that factors other than duration of ice cover and water temperatures are important.

The Iceland Cockle also displayed its most intense escape behaviour towards the sea stars *L. polaris* and *A. rubens,* two of its primary predators (Legault and Himmelman 1993). This cockle rarely burrows more than 4 cm from the substrate surface and it too must rely on its escape behaviour to limit predation.

Relation to Man

Serripes groenlandica has been used as a bioindicator species, specifically in the study of the effects of exposure to oil in the Canadian Arctic (Humphrey *et al.* 1987; Cross and Thomson 1987; Gilfillan and Vallas 1984). Sauve *et al.* (2002) monitored the phagocytic activity of marine and freshwater bivalve haemocytes in response to exposure to various metals.

3.3.9 Northern Horse Mussel (*Modiolus modiolus*)

General Distribution

The Northern Horse Mussel is a circumpolar species with a distribution in the northwestern Atlantic Ocean extending south to the Long Island region. This species may occur as high as the lower intertidal zone, but primarily inhabits the shallow subtidal zone (Gosner 1979). It has been found to occur as deep as 280 m. These mussels tend to prefer stable substrates (rock/stable gravel) suitable for byssal attachment. *Modiolus modiolus* has been referred to as a "key structural species" or an "ecological engineer" because a bed of this mussel provides a distinctive

habitat and its loss would likely lead to the disappearance of the associated community (Hiscock *et al.* 2004).

Life Cycle

Spawning and Fertilization: The spawning season of this mussel is not well defined mainly because timing varies widely with depth and geographic location. Horse Mussels in Norway generally spawn: once during March and April, while those in the Bay of Fundy typically spawn twice; once during the March to May period and once during the August to October period. It is believed that major synchronized spawning events may not occur annually in this species, but partial spawning does occur each year. It can be up to five years between major spawning events (Caddy *et al.* 1977).

Fertilized Eggs and Larvae: Fertilized eggs obtained by De Schweinitz and Lutz (1976) ranged in diameter from 78 to 90 µm. When fertilized eggs were cultured at 16 to 21 °C, the time between fertilization and initial larval settlement was 19 days.

Northern Horse Mussel larvae were collected on the southern New England Shelf between late July and December over a depth range of 10 to 40 m. The highest concentrations of Horse Mussel larvae were found during the August to October period. Water temperatures in this part of the water column ranged from 14 to 18 °C during the April to October period. The Horse Mussel larvae were abundant along with larvae of the Ocean Quahog (*Arctica islandica*) and Atlantic Surfclam (*S. solidissima*) (Mann 1985).

Juveniles and Adults: The Horse Mussel is a sessile suspension feeder. Lesser *et al.* (1994) concluded that the concentration of, rather than the flux of seston is most important to the Horse Mussel in terms of its scope for growth and biomass. Seston includes living plankton, organic detritus and inorganic particles. The quantity of this suspended particulate matter and its quality as food for suspension feeders vary both temporally and spatially in response to physical and biological factors. These factors include biological production, periodic storms, wind-wave resuspension and tidal resuspension. Navarro and Thompson (1995) studied the seasonal fluctuations of seston available to Horse Mussels in the subarctic environment at Logy Bay, Newfoundland during a two-year period. Biodeposition by Horse Mussels at Logy Bay was also studied during that same period (Navarro and Thompson 1997). They concluded that the release of considerable amounts of energy rich pseudofaeces by these mussels during the peak of the spring diatom bloom might provide a pulse of organic material available to grazers in the water column and ultimately to the suspension feeders and deposit feeders of the benthos. This would be particularly evident in rocky shore environments where Horse Mussels tend to occur in dense concentrations.

During investigations of the effect of substrate type on Horse Mussel growth rates, Wildish *et al.* (2000) attempted to test the hypothesis that tidal and/or wind-wave induced flows inhibit initial feeding by Horse Mussels. Their experimentation was not conclusive due to conflicting results (i.e., effect on exhalant siphon opening supported the alternative hypothesis, but effect on seston depletion supported the null hypothesis). Wildish *et al.* (2001) determined skimming flow does not reduce Horse Mussel growth rates. Read and Cumming (1967) found that the lethal

maximum water temperature for Horse Mussels examined in Massachusetts was approximately 23 °C, while they have high tolerance for low water temperatures (i.e., 0 to < 5 °C). Caddy *et al.* (1977) reported the minimum lethal salinity limit for Horse Mussels at 20 to 25 ppt.

Wildish *et al.* (1998a) presented some possible limiting factors that influence the development of Horse Mussel populations. They included: 1) the presence of a solid, non-moving substrate; 2) the presence of a suitable flux of sestonic food not too "diluted" with saltating sand which reduces its food value; 3) the absence of excessive hydrodynamic forces which cause inhibition of initial feeding; 4) different roughness elements on the seabed which cause changes in benthic boundary layer flows and therefore disturbances in sestonic food delivery; and 5) the presence of predators. These limiting factors would operate at larval settlement as well as post-settlement stages of the Horse Mussel life history. In a shallow tidal channel at Bellevue Newfoundland, a dense, high biomass mixed bed of Horse Mussels and Blue Mussels has been observed (K. Gilkinson, D. Methven, unpubl. data). Although peak tidal current speeds were high (approx. 1 m/sec), the bed was stable due to combined mass and mutual attachment by byssal threads.

Ojeda and Dearborn (1989) studied the community structure of the macroinvertebrate fauna inhabiting a rocky subtidal habitat in Maine. Along with the Green Sea Urchin, Horse Mussels were consistently one of the most important assemblage components in terms of biomass and density. Horse Mussels increased in abundance with depth (from 5 to 18 m). The distributions and abundance patterns of other benthic macroinvertebrates were strongly influenced by the spatial distributions of Horse Mussels. Comparative analysis showed that at 18 m depth, invertebrate fauna within the Horse Mussel beds were significantly more abundant, dense and diverse than outside the beds. Therefore, the Horse Mussels provide spatial refuges from predators and suitable, stable microhabitats for numerous invertebrates. Similarly, the mixed mussel bed studied by Gilkinson and Methven (1991) in a tidal channel at Bellevue, NL also supported a diverse and abundant invertebrate community that likely would have been absent otherwise. Despite their low primary productivity, typified by those in rocky habitats of Maine, Horse Mussel-dominated coralline communities are ecological systems with relatively high species diversity and secondary productivity.

Work carried out by Witman (1987) in the Gulf of Maine appeared to demonstrate a mutualistic interaction between Horse Mussels and Green Sea Urchins. Urchin grazing seemed to control kelp growth, thereby minimizing mussel mortality due to kelp overgrowth. At the same time, the mussel beds appeared to provide a more stable substrate for urchin attachment, thereby making the urchins less susceptible to predation and dislodgement-caused mortality than those located outside of the mussel beds.

In New Brunswick, Logan (1988) described the Horse Mussel association with tubularian hydroids and anemones within a sublittoral hard substrate epibenthic community deeper than 30 m. Horse Mussel beds appear to be effective faunal refuges because they persist for many years and resist biotic disturbance. Witman (1985) examined subtidal communities in New Hampshire and results demonstrated the functional significance of mussel beds in cold-temperate subtidal regions where predation and sea urchin grazing are major determinants of community organization. Hiscock *et al.* (2004) indicated that beds of *M. modiolus* provide structures that

support a wide range of species and could possibly function as important nursery areas for scallops.

In areas such as the lower Bay of Fundy, tidal currents are a major determinant of benthic distribution and production (Wildish *et al.* 1981). Wildish and Peer (1981) concluded that the Horse Mussel was by far the largest contributor to the approximately 88% of production attributed to suspension feeders in the area. The tidal currents control sediment dynamics as well as settlement, growth and feeding of benthic animals. Wildish *et al.* (1998b) described Horse Mussel reefs found in the upper Bay of Fundy during acoustic surveys. Their linear shape, distribution and orientation suggested a dominant control by strong tidal currents.

The Horse Mussel has been identified as a key animal species of a biota assemblage associated with the "coralline algal bed" characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. Physical characteristics attributed to this habitat type include bedrock/boulder substrate with patches of round coralline balls and sediments, moderate to high exposure to wave energy, high salinity and generally strong currents (Hooper 1997). Coralline algal beds are extremely common around Newfoundland and Labrador.

Keats *et al.* (1986a) examined the diets of ninety wolffish collected from a sea urchin- dominated rocky subtidal habitat in eastern Newfoundland. Horse Mussels accounted for almost 10% of the diet by weight, second only to sea urchins (76%). Other major predators of the Horse Mussel include American Lobster and Rock Crab (Jamieson *et al.* 1982; Hudon and Lamarche 1989).

Relation to Man

Even though there is no directed commercial fishery for this mussel species, it fills the ecological role as an important prey item for commercially important species such as the American Lobster (Elner and Campbell 1987). The Horse Mussel has also been considered as a bioindicator, specifically for monitoring zinc and manganese levels (Chou *et al.* 2003a).

3.3.10 Blue Mussel (*Mytilus edulis*)

General Distribution

The Blue Mussel has a circumpolar distribution and occupies temperate waters. In the northwestern Atlantic Ocean, its distribution extends from the Arctic to South Carolina. This bivalve can be found in habitats ranging from slightly brackish, shallow estuaries to highly saline offshore environments. In Newfoundland, Blue Mussels are most commonly found in the intertidal and shallow subtidal zones (< 20 m) (DFO 1996d). Barrie (1979) found these mussels along Newfoundland and Labrador coasts at depths ranging from 1 to 62 m. Carscadden *et al.* (1989) reported a population of large Blue Mussels on the Southeast Shoal of the Grand Bank. This population is one of the world's few deeper water subtidal populations and the one furthest from shore.

In the mid-1980s, conclusive proof was presented which demonstrated the presence of a closely related species (*Mytilus trossulus*) in Nova Scotia (Freeman *et al.* 1992). It was later determined that the mussels *Mytilus edulis* L. and *M. trossulus* Gould are found sympatrically in most areas

of Newfoundland, with a low frequency of hybrids (Toro *et al.* 2002). Prior to this, it was thought that populations of *Mytilus* were comprised entirely of *M. edulis* (DFO 1997b).

Life Cycle

Spawning and Fertilization: Spawning by this dioecious species and subsequent external fertilization generally occurs during the May to August period, peaking between mid-May and late June. Spawning appears to occur in response to environmental triggers, including sufficiently high water temperatures (10 to 12 °C), suitable planktonic food supply, spring tidal currents and sudden physical disturbance during storms. Salinity should be at least 15 ppt to ensure successful fertilization (Bayne 1976). There is evidence for phytoplankton-sourced chemical stimuli that trigger the spawning process (Starr *et al.* 1990). Female Blue Mussels can release between 3 and 20 million eggs (Mallet and Myrand 1995).

Normally, gametogenesis occurs slowly during the winter months, accelerating with the onset of the spring phytoplankton bloom. Lowe *et al.* (1982) showed how high summer temperatures may cause disturbance to the gametogenetic rhythm of Blue Mussels. A mussel population studied in Britain exhibited the concurrent occurrence of gametogenesis and development of storage reserve tissue that resulted in a second spawning in the same year.

It has been suggested that animals such as bivalves, unable to predict environmental quality for their juveniles, should have long adult life, but low and variable reproductive effort. Thompson (1979) observed annual variability in Blue Mussel fecundity in populations in Newfoundland and Nova Scotia. He found that reproductive effort was consistently high despite the inter-annual variability in fecundity. Toro *et al.* (2002) studied reproductive aspects of two mussel species living sympatrically in most areas of Newfoundland, *M. edulis* and *M. trossulus*. They found that *M. trossulus* and hybrids of the two species spawned over a prolonged period from late spring to early fall, while *M. edulis* tended to spawn over a 2 to 3 week period in July. *M. trossulus* had a higher reproductive output and smaller eggs than *M. edulis*.

Fertilized Eggs and Larvae: Fertilized eggs of the Blue Mussel are benthic and require temperatures of at least 5 °C for proper development. Food availability is especially important upon larval hatch. The initial larval stage is the trochophore stage. The trochophore develops into the veliger stage which eventually exhibits a shell and foot. In Atlantic Canada, Blue Mussel veliger larvae are often among the first invertebrate larvae to be caught in plankton tows during the spring (Mallet and Myrand 1995). The free-swimming larvae remain planktonic for 3 to 4 weeks before settling. The duration of the planktonic life stage is primarily dependent on water temperature, salinity and food level. Although capable of vertical migration, Blue Mussel larvae are essentially at the mercy of currents and may be carried considerable distances from the spawning area. In Atlantic Canada, settlement can occur at any time from mid-June to late September, generally peaking during the mid-June to late August period. Pryor and Parsons (1999) and Pryor *et al.* (1999) indicated that mid-July was often the peak settlement time on some mussel farms in Newfoundland where typical water temperatures and salinities at that time were 16 to 17 °C and 28 to 29 ppt, respectively. Freeman (1974) found that maximum spat settlement at two locations in Nova Scotia occurred at depths ranging from 0.5 to 3 m. The larvae are typically 250 to 300 µm in length at time of settlement and appear to be most

successful on substrate with surface irregularities and areas with some protection from strong wave action. Other features that attract larvae to certain substrates may include chemical cues (Coon *et al.* 1985) and the byssal threads of previously attached mussels (Lutz and Kennish 1992). Once the larvae settle, crawl and eventually attach to the substrate by byssal threads, they metamorphose into young-of-the-year juveniles (spat). Development into spat can be delayed for up to a month until environmental conditions are most suitable (Freeman 1974).

Brenko and Calabrese (1969) studied the combined effects of salinity and temperature on the survival and growth of Blue Mussel larvae. The effects of the two parameters were significantly related only when the limits of tolerance of either one were approached. There was at least 70% survival within a salinity range of 15 to 40 ppt and temperature range of 5 to 20 °C; however, at 25 °C, survival declined at salinity extremes of 20 ppt and 40 ppt. Optimum larval growth occurred at 20 °C with salinities between 25 and 30 ppt. Growth decreased at temperature extremes of 10 °C and 25 °C, especially at the high and low ends of salinity tolerance. Bayne (1965) found differences in growth rate between Blue Mussel larvae in the littoral and sublittoral zones at temperatures greater than 18 °C. Specifically, those from the littoral zone showed an increase in growth rate, while those from the sublittoral zone exhibited a decreased growth rate. He also found that larvae from an area of full salinity had a narrow range of optimal salinity for growth (30 to 33 ppt), while those from areas of reduced salinity had a lower range of optimal salinity and a greater tolerance range. In other words, acclimation is important in assessing the effects of temperature and salinity on larval growth.

Roegner (2000) discussed the transport of molluscan larvae through a shallow estuary in Nova Scotia. He found that in certain estuarine systems, tidal flow is too substantial for the larvae not to be exported from the hatching area to the coastal ocean. Therefore, the temporal persistence of the Blue Mussel in such estuaries is probably dependent on larval invasion. It is likely that many estuaries in an area contribute to a larval pool residing in the nearshore zone which, in turn feed the estuaries under appropriate oceanographic conditions.

Blue Mussel veligers, as well as juveniles and adults, filter feed on plankton and detritus. Raby *et al.* (1997) investigated food particle size and selection by bivalve larvae, including Blue Mussel veligers, in the Baie des Chaleurs, Gulf of St. Lawrence. September sampling was conducted at 2 to 14 m below the surface at a 20 m deep site located approximately 3 km offshore. The water column was well mixed from top to bottom. Blue Mussels and Softshell Clams dominated the veliger community. They found that Blue Mussel veligers preferentially fed on 15 to 25 µm algal cells, especially the larger larvae (261 to 405 µm), demonstrating that selected food size increases with veliger size. In turn, Blue Mussel larvae are prey to zooplankton and small fish feeding near the surface.

Juveniles and Adults: Sessile spat prefer stable, hard substrates (i.e., bedrock/boulder, wharf pilings) for attachment. The location of attachment must also have sufficient water movement to allow movement of food, nutrients and waste. Kelp harvesting can impact mussel larval settlement by reducing the amount of substrate for attachment. The juvenile mussels can easily detach themselves and change locations, either by using their foot to actively crawl or by floating passively in the water column. Movement becomes increasingly limited as the mussels become heavier (Mallet and Myrand 1995).

A study in Rhode Island demonstrated that *M. edulis* byssal attachment strength (tenacity) increases twofold in the winter compared to summer (Carrington 2002). Time series analysis of monthly samples indicated that tenacity was correlated with seasonal fluctuations in wave height, suggesting that mussels sense and respond to changes in their flow environment. At the same time, Carrington (2002) suggested that tenacity was reduced somewhat during the period of gonad development.

Hooper (1997) described the Blue Mussel as a key animal species of the biotic assemblage generally associated with a habitat type called "lobster grounds" found in coastal marine areas of Newfoundland. Physical characteristics of this habitat type include mixed substrates with suitable rocks for lobster burrows, generally full salinity, a wide range of affecting currents, areas with relatively warm summer water temperatures and a full range of exposure to wave energy (Hooper 1997). Gilbert *et al.* (1984) described a sea-ice controlled coastal environment near Nain, Labrador in which the Blue Mussel was the dominant mollusc. The Blue Mussel occurred on the intertidal flats at the boulder barricade and associated tide pools near the outer edge of the flats area. Himmelman (1991) reported the occurrence of Blue Mussels in the lower intertidal zone of three types of intertidal/subtidal regions in the northern Gulf of St. Lawrence: 1) moderately exposed, medium-sloped bottom, 2) exposed, gently sloping bedrock platform and 3) rocky faces.

The affect of two contrasting environmental regimes (coastal and estuarine) on aspects of the biology of *M. edulis* and *M. trossulus* from Newfoundland were examined by Gardner and Thompson (2001). Environmental parameters measured included water temperature, salinity, total particulate matter and particulate organic matter. The biological parameters monitored included: mortality rate, energy acquisition, biochemical composition and specific growth rate. Results of the study indicated that *M. edulis* was better adapted to conditions of low and/or fluctuating salinity. Sullivan (2004) examined byssal thread production and locomotion in *M. edulis* under varying salinity, temperature and feeding conditions.

Bergeron and Bourget (1986) studied the effect of substrate heterogeneity on the distribution and abundance of sessile epibenthos on a mid-intertidal shore subject to severe annual ice scouring. In summer, they found low abundances of organisms associated with the smooth regular surfaces, whereas there were high abundances of organisms, including Blue Mussels, in the cracks and crevices of the substrate. The Blue Mussels tended to occupy the lowest region of the crevices, while barnacles and rockweed occurred immediately above.

The ability of mussels to grow and reproduce under a wide range of environmental conditions is largely responsible for their worldwide distribution (Seed 1969). Juvenile and adult Blue Mussels can tolerate a salinity range of 0 to 31 ppt, although growth rates are severely affected at each extreme of the range. Optimal growth occurs around a salinity of 26 ppt (Mallet and Mynard 1995). Little growth occurs below and above water temperatures of 0 °C and 20 °C, respectively. Bourget (1983) reported that juvenile Blue Mussels in the St. Lawrence Estuary showed a lower cold tolerance (–8 to –12 °C) than adult mussels (-12 to –20 °C). The median lethal temperatures varied seasonally due to the variability in salinity. Loomis (1995) reported that this bivalve is able to withstand temperatures far below zero and that its freezing tolerance is increased if it is acclimated to high salinity.

Blue Mussel stress responses to seasonal and/or environmental changes were investigated by Harding (2003) using animals collected from various mussel aquaculture sites in Newfoundland. Some of the stressors used in her study included water temperature, food availability and exposure to air. The mussels appeared stressed when exposed to water temperatures outside the normal range, air temperatures more than 5 °C from ambient water temperature and when denied food. Harding (2003) found that the Blue Mussels in her study were in best physiological condition between late autumn (December) and spring (May). Read and Cumming (1967) concluded that the lethal maximum water temperature for Blue Mussels studied in Massachusetts was approximately 23 °C. Although physical conditions such as temperature and salinity may affect growth, food supply is the primary determinant.

Phytoplankton cells, both living and dead, constitute the primary source of organic matter for mussel growth. Other food items include bacteria and dissolved organic molecules (Mallet and Mynard 1995). Wong and Levinton (2004) demonstrated by a microcosm study that a mixed diet of phytoplankton and zooplankton yielded better growth and metabolism in *M. edulis* than diets of each separately. In Quebec, lobster fishermen were concerned that mussel aquaculture might pose a threat to lobster, by the mussels ingesting or otherwise killing lobster larvae (Gendron *et al.* 2003). A study was conducted to investigate this issue, which the results did not support.

Predators of the Blue Mussel include sea ducks (Guillemette *et al.* 1992), sea stars (Miron *et al.* 2002), lobster and crabs (Miron *et al.* 2002). Fouling organisms such as algae and anemones may compete directly with mussels for food or even suffocate the mussels by reducing water circulation through and over the mussel clump. The Blue Mussel is the most important food item for the common eider, *Somateria mollissima*. The results of a study by Bustnes (1998) strongly indicated that eiders selected primarily subtidal-zone mussels with the lowest shell mass, thereby minimizing intake of the indigestible shell.

Relation to Man

Adult Blue Mussels have been an ideal bioindicator species for marine environmental quality mainly because it is a sessile filter feeder. Freeman and Dickie (1979) demonstrated the potential of using growth and mortality rates of Blue Mussels as a sensitive measure of relative productivity and environmental quality between areas. Biomarker responses in Blue Mussels have also been investigated as a means of pollution effect indication in Scandinavian countries (Barsienė *et al.* 2003; Lehtonen *et al.* 2003). Conversely, Chou *et al.* (2003b) made a case for the deficiencies of Blue Mussels in monitoring the environment. They used Blue Mussels, American Lobsters (*Homarus americanus*) and sediments as indicators of contaminants in the coastal environment of the Bay of Fundy. They concluded that both Blue Mussels and sediment were ineffective as reliable bioindicators and that lobsters were a much better choice. Feist *et al.* (2002) measured histological changes in Blue Mussel tissue as a result of exposure to various contaminants. They concluded that observed tissue changes might indicate the usefulness of Blue Mussels as environmental sentinels, particularly for biological effects monitoring studies in the proximity of oil platforms.

As early as 1968, Blue Mussel beds in Newfoundland were assessed for harvesting potential (Scaplen 1970). The Marine Sciences Research Laboratory, Memorial University of Newfoundland, conducted surveys in Bonavista Bay to determine the extent of Blue Mussel beds

there. Investigators found numerous beds that seemed to represent considerable commercial fishery potential.

In 2000, almost 100 licenses were issued in Newfoundland for Blue Mussel aquaculture. The highest concentration of mussel farms in Newfoundland is in Notre Dame Bay, but farms are also scattered along the coastline. In 2005, almost 3,157 t of mussels were produced by the Newfoundland aquaculture industry (DFA 2006).

3.3.11 Iceland Scallop (*Chlamys islandica*)

General Distribution

The Iceland Scallop is a subarctic-boreal species with a northwest Atlantic Ocean distribution extending from Hudson Strait, Northwest Territories south to the Massachusetts region. Its bathymetric range is from relatively shallow subtidal depths to about 180 m (Lubinsky 1980; Black *et al.* 1993). Newfoundland populations of the Iceland Scallop are typically found at depths exceeding 55 m on hard substrates of variable composition, including mixtures of sand, gravel, shell fragments, rocks and boulders (Naidu 1988; Gilkinson and Gagnon 1991). Based on these depth preferences, Iceland Scallops in Newfoundland and Labrador prefer high salinity (> 18 ppt) and are not usually exposed to wave energy. Being a filter feeder, this species is most abundant in areas with strong currents. Iceland Scallops occur in dense, commercial concentrations on St. Pierre Bank (Newfoundland Grand Banks) (Naidu and Cahill 1989). Iceland Scallops thrive in waters associated with strong currents and water temperatures ranging from –1.5 to 8.0 °C (Galand and Fevolden 2000).

Life Cycle

Spawning and Fertilization: Unlike many species of scallops, the Iceland Scallop is dioecious. Scallops in Icelandic waters reach sexual maturity at 3 to 5 years of age (Crawford 1992). Broadcast spawning in Newfoundland normally begins around April or May, possibly triggered by short-term variations in water temperature (DFO 1997c). Spawning by Iceland Scallops in the northern Gulf of St. Lawrence typically occurs during the July to August period (Arsenault and Himmelman 1998b), apparently coinciding with the phytoplankton bloom. Around the Magdalen Islands (southern Gulf of St. Lawrence), the spawning period is normally between July and September (Giguere *et al.* 1993; 1994). Females are highly fecund and produce millions of eggs that undergo external fertilization in the water column.

Fertilized Eggs and Larvae: Fertilized egg development time is a matter of hours before larval hatch occurs. The trochophore larva is the hatching stage and this develops into the veliger stage prior to settlement (Crawford 1992). *Chlamys islandica* larvae are planktonic for up to 10 weeks before settling onto substrates consisting of shell debris and filamentous materials (Vahl 1982). Settlement is gregarious, sometimes resulting in densities of settled animals of up to 100 individuals/m^2. Harvey *et al.* (1995) observed settlement in the Baie des Chaleurs (northern Gulf of St. Lawrence) between mid-September and mid-October. Harvey *et al.* (1993) found that post-larval Iceland Scallops were twenty times more abundant on dead hydroids than on normally preferred live hydroids and red algae. Chemical cues likely mediate the settlement behaviour of Iceland Scallops.

Garcia *et al.* (2003) investigated the seasonal pattern of bivalve spat settlement in North Iceland using artificial collectors over a 14-month period. Their results indicated that *C. islandica* settled primarily between August and November, with peak settlement in September. The collectors at 10 m had the greatest abundance of Iceland Scallop spat, followed by those at 15 m. The mean water temperature in September was about 8 °C and by November it had dropped to about 4 to 5 °C.

Juveniles and Adults: Arsenault and Himmelman (1996a; 1996b) studied the spatial distribution of Iceland Scallops in a non-harvested population in the northern Gulf of St. Lawrence. Size partitioning related to depth was evident with a predominance of small scallops (< 30 mm shell height) at 15 m and mainly larger scallops (> 60 mm) at 30 m. Legault and Himmelman (1993) suggested that the low abundance of large individuals in shallow water might be due to the concentration of predators at these depths, specifically sea stars and Waved Whelks. Zolotarev (2002) also observed predation on Iceland Scallops by sea stars. Most small scallops were found in crevices under bivalve shells or rocks. They proposed that size partitioning in that particular population resulted from higher settlement and survival in shallow water, followed by a gradual down slope movement with increasing scallop size. Arsenault *et al.* (2000) provided the first experimental evidence supporting the controversial hypothesis of recruitment into adult scallop populations involving swimming of juveniles from the upslope nursery areas. It is hypothesized that Iceland Scallops are aggregated on coarse substrates because of a strong propensity towards byssal attachment at all post-larval life history stages. This propensity for adult byssal attachment to coarse substrates is an evolutionary adaptation for a sessile existence revealed in morphological characteristics of this species. Byssal attachment is a common trait in this genus (Gilkinson and Gagnon 1991). Those that settle on softer substrates are capable of blowing out depressions in the bottom where they lie and avoid bottom current effect (Crawford 1992).

Oganesyan (1994) found Iceland Scallops on a variety of substrate types, including silt/sand, rock/shell, boulder/stone/shell and rock/silt. All were found within a depth range of 50 to 100 m. The areas of occurrence on St. Pierre Bank have sediments consisting of a mixture of gravel (> 90%) and sand (< 10%) (Fader *et al.* 1982). Gilkinson and Gagnon (1991) found that Iceland Scallops on the northeastern Grand Bank of Newfoundland were associated primarily with the coarsest grade substrate consisting of gravel and cobble. They were rare on the predominantly sand substrate found in the study area.

Arsenault *et al.* (1997) and Arsenault and Himmelman (1998c) found that using substrate and debris for refuge by small scallops (15 to 30 mm shell height) enhanced their growth rates, but did not appear to have any impact on the larger scallops (30 to 60 mm shell height). Despite this, they concluded that the tendency for scallops to seek refuge does not change during ontogeny, but that availability of refuge decreases with scallop growth.

Although growth rates vary from area to area, on average it takes about 7 or 8 years for an Iceland Scallop to reach commercial size (65 mm shell height), while it takes 3 to 6 years to reach sexual maturity. These animals frequently live in excess of 25 years, but seldom exceed 100 mm shell height (DFO 1997c). Frechette and Daigle (2002a) reported results from a modeling study that investigated the effects of factors such as boundary layer current speed and the resuspension of inorganic particles near the bottom on the growth of Iceland Scallops

cultured near the bottom in pearl nets. They found that both factors have some influence on the quality and quantity of seston available to the scallops. These authors also conducted a field experiment designed to look at various factors that might affect Iceland Scallop growth (Frechette and Daigle 2002b). Soft tissue growth was slowest and survivorship lowest in the scallops set in pearl nets near the bottom compared to those suspended higher in the water column.

Iceland Scallops located on the western Grand Banks of Newfoundland are catastrophically susceptible to sea star predation (Naidu *et al.* 1999). *C. islandica* may be most susceptible to predation during gonad maturation and spawning because of slower recuperation from exhausting burst exercise (i.e., valve clap escape response) (Brokordt *et al.* 2000). It appears that the adductor mussel may have decreased metabolic capacity during these reproductive stages.

Relation to Man

Preliminary data (DFO 2007a) indicate that during 2006, almost 1,825 mt of Iceland Scallops were landed in the Newfoundland Region at a value of just over $2.4 million. DFO Reports (2001a; 2007c) indicate that most Iceland Scallop removals are from the Strait of Belle Isle, off the southwest Avalon Peninsula, Placentia Bay, St. Pierre Bank and Lilly/Carson Canyon in NAFO Division 3N. The 2006 landings were down from a recent high in 1998 when 6,700 mt were landed in the Newfoundland Region, valued at over $10 million.

3.3.12 Sea Scallop (*Placopecten magellanicus*)

General Distribution

Sea Scallops are distributed in the northwest Atlantic Ocean from Labrador to Cape Hatteras, North Carolina. In the northern part of their range, they tend to occur in shallow water at depths of less than 20 m, while in the southern portion of their range, Sea Scallops are normally found in water deeper than 55 m. In Newfoundland and Labrador, they are generally distributed throughout the shallow coastal region of insular Newfoundland occurring most often on sand-gravel or gravel-pebble substrates (Mullen and Moring 1986; DFO 1988; Black *et al.* 1993; DFO 1996e; 1998c). Three localized aggregations of Sea Scallop exist on St. Pierre Bank concentrating on soft substrates (DFO 2007a).

Life Cycle

Spawning and Fertilization: Sea Scallops are normally dioecious and their spawning times vary from July to early October, depending on location (Beninger 1987). Kenchington *et al.* (1991) hypothesized that certain inshore populations in Nova Scotia may exhibit springtime spawning. Spawning time tends to be later as one moves north within the distribution range. In Newfoundland, Sea Scallop spawning typically occurs in September and October, specific timing being dependent on latitude and environmental conditions. Naidu (1970) observed a minor spawning episode of Sea Scallops in Port au Port, Newfoundland and reported bottom water temperatures during spawning range from 4 to 14 °C for a period of 1 to 5 weeks. Posgay (1979) suggested that fall spawning of Georges Bank scallops might be triggered by a rise in bottom water temperature that follows thermocline breakdown. Other suggested spawning triggers include tidal cycles (Dickie 1955) and prolonged exposure to physical shocks such as

rough seas caused by strong onshore winds (Naidu 1970). Sea Scallops are highly fecund, with large females capable of producing well over one hundred million eggs and males several billion sperm (Couturier *et al.* 1995). There is a strong positive association between female size and fecundity. Fertilization of Sea Scallop eggs is external, occurring in the water column immediately above the scallop bed. Desrosiers *et al.* (1996) investigated the effects of temperature, salinity and pH on various stages of Sea Scallop fertilization. The observed conditions most favourable for fertilization, meiotic maturation and first zygotic cleavage were a water temperature of 10 °C, salinities ranging from 25 to 28 ppt and a pH range of 8.0 to 8.5.

Fertilized Eggs and Larvae: The pink and brown fertilized eggs are approximately 64 μm in diameter and are planktonic. At 15 °C and 32 ppt salinity, the embryos develop to hatching larvae within 2 to 3 days. The planktonic larvae are initially about 69 μm long, but by the fourth day after hatching, the larvae have developed into shelled straight-hinge veligers of an average length of 105 μm. Culliney (1974) described in detail the development of larvae from hatch to end of planktonic stage. Once the larvae grow to approximately pinhead size (~ 4 weeks), they develop a "foot" from which a byssus can be produced. The byssus is used to attach the animal to a substrate (gravel, shells or plants) upon settlement to the benthic environment. Planktonic Sea Scallop larvae may be transported out of the spawning area by predominant currents. Therefore, many of the scallop populations may not be self-populated by their own larvae and spat. At settlement, the spat tend to attach themselves to the underside of shell fragments and other solid materials on the bottom, perhaps as a way to counter predation. The larvae are able to delay settlement and metamorphosis for approximately one month while they search for suitable substrate. After settlement, the post-larval scallops are found on various substrate types, but seem to prefer firm gravel and cobble areas with good water exchange to maximize food and oxygen availability (Hawkins 1996).

The eggs and larvae require uncontaminated seawater within a particular temperature range and the larvae also require an adequate planktonic food supply. Under laboratory conditions, larvae grew well at a water temperature of 15 °C, but showed high mortality at 19 °C. They appear to be euryhaline, surviving at salinities as low as 10.5 ppt (Hawkins 1996). Tremblay and Sinclair (1990) studied the vertical distribution of Sea Scallop larvae over a two-day period in the Bay of Fundy. They observed the larvae as deep as 11.5 m during the day and within 4 m of surface during the night and also found that within 8 m of the bottom, the concentration of Sea Scallop larvae was greatly reduced.

While Sea Scallop larvae feed on phytoplankton, they themselves are vulnerable to predation by a wide variety of planktivores. Work by Feindel (2000) in Newfoundland supported the hypothesis that the fatty acid profile of a standing phytoplankton crop can impact the growth and settlement success of Sea Scallop larvae. Another Newfoundland study conducted by Ryan (2000) found that algal cell density had an affect on growth and survival and particular algal species were preferred by the larvae and spat, regardless of algal cell size similarity.

Raby *et al.* (1997) investigated food particle size and selection by bivalve larvae, including Sea Scallop veligers, in the Baie des Chaleurs, Gulf of St. Lawrence. The September sampling was conducted 2 to 14 m below the surface at a 20 m depth location approximately 3 km offshore. The water column was well mixed from top to bottom. Blue Mussels and Softshell Clams

dominated the veliger community. They found that Sea Scallop veligers along with the Blue Mussel veligers within the 185 to 260 μm size range ingested more < 5 μm and 5 to 15 μm algae than the Softshell Clams.

Juveniles: Generally, Sea Scallops are in the juvenile stage (i.e., sexually immature and benthic) for approximately one year. By the onset of their first winter, Sea Scallops are approximately 5 mm shell height. Byssal attachments are lost as the scallops grow larger and eventually the scallops begin to lie freely on the bottom. As juveniles and young adults, Sea Scallops are relatively efficient swimmers and respond with this behaviour to disturbances such as predation threats and commercial dredging. Although sexual maturity is normally reached by 1 to 2 years of age, time to maturity varies between locations (Mullen and Moring 1986).

Barbeau *et al.* (1996a) examined the dynamics of juvenile Sea Scallops and their invertebrate predators in bottom seeding trials in Nova Scotia. They found that predation was the major cause for loss of seeded scallops. Their observations suggested that crabs were more important invertebrate predators than sea stars (Barbeau *et al.* 1996b). Survivorship of the Sea Scallops was higher at the topographically open site (~ 10%) than at the enclosed site (~ 1%). Hatcher *et al.* (1996) demonstrated the potential for ecologically viable bottom culture of Sea Scallops through a seeding study in a Nova Scotia tidal channel. Thirteen months after seeding, the scallop density increased to twice that of the natural population. Hatcher *et al.* (1996) identified four phases in the trajectory of the scallop population during the 13 months following seeding: 1) sorting phase for the first few hours during which highly aggregated scallops separated themselves and attached to the substrate; 2) mortality and dispersion phase over the first few days to weeks during which predation was severe and frequent long swims produced large individual displacements and rapid horizontal diffusion of the population; 3) stable phase for several months during the winter when predation mortality was low and dispersion slowed; and 4) dispersion phase extending through the summer and autumn when displacement increased to produce a uniform, low density of scallops that experienced little further mortality.

Kenchington *et al.* (1991) conducted preliminary investigations of juvenile Sea Scallops in Nova Scotia inshore habitats. A preference for gravel substrate was indicated from their survey, although there was some evidence of juvenile scallop seasonal movement between areas of differing substrate and depth (i.e., silty area in early summer and gravel area in the fall). However, this speculation regarding seasonal movement needed further investigation.

Newly settled Sea Scallops were collected from Georges Bank in February and May (Larsen and Lee 1978). The two densest post-larval Sea Scallop beds were found during February at 77 and 165 m depths. The bottom temperatures at these two stations were 4.9 and 8.0 °C, respectively. Salinities at both stations were between 34 and 35 ppt. The three next densest beds were in depths ranging from 76 to 84 m, at bottom temperatures ranging from 5.0 to 6.4 °C and salinities around 34 ppt. Juveniles exposed to a salinity of 21 ppt acted normally.

Adults: Large adult scallops (~ 9 cm shell height) are typically recessed in the sediment and do not usually move unless physically disturbed. Sea Scallops older than 20 years are frequently observed in areas of low exploitation. Where conditions are favourable, scallops frequently occur in dense local populations known as "beds" (DFO 1989a). Occurrence of a "bed" in a

specific area depends on the chance of larval settlement in that area and the subsequent survival rate of a large number of spat. Environmental conditions and predator presence, dictate both.

The Sea Scallop has been identified as a key organism in the "scallop bed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat for Newfoundland and Labrador. This scallop is often associated with kelps and other fleshy seaweeds. The geology of this habitat type generally includes sand or fine gravel and other characteristics typically include warm summer water temperatures and minimal exposure to wave energy (Hooper 1997). In Newfoundland, Sea Scallop beds are most abundant in shallow sheltered sandy locations such as Port au Port, Salmonier Arm, Long Harbour and western Placentia Bay. Dense hydroid growth on live Sea Scallop shells is commonly observed (Henry and Kenchington 2004).

The high lethal temperature for adult Sea Scallops ranges from 20 to 24 °C, depending on the acclimation temperature. A sudden rise in water temperature can induce high mortality in a scallop bed. Optimal growth seems to occur at about 10 °C. MacDonald and Thompson (1985a; 1985b; 1986) studied the influence of water temperature and food availability on the ecological energetics of large juveniles and adults of all sizes from various locations in Newfoundland. Generally, they found that shallow water areas (6 to 10 m depth) were more favourable for shell growth, somatic growth and gonad production than deepwater areas (> 30m). Sea Scallops normally reach sexual maturity at two years of age.

Adult scallops filter feed on plankton and detritus. Cranford and Grant (1990) demonstrated the importance of phytoplankton in the diet of Sea Scallop, but results also indicated that detrital particles can contribute to energy gain during periods when phytoplankton is less available. The presence of inorganic suspended solids can adversely affect Sea Scallops by interfering with normal feeding. Cranford and Gordon (1992) reported on the influence of dilute clay suspensions on scallop feeding activity and tissue growth. There is also evidence for simultaneous post-ingestive sorting of food particles by *Placopecten magellanicus*, based solely on the chemical properties of the food particles (Brillant and MacDonald 2002). This would potentially enable Sea Scallops to preferentially retain particles of higher food quality longer than those of poor quality, thereby enhancing digestive efficiency. Andrews (2000) studied the effect of fouling and current velocity on the feeding rate of *P. magellanicus* in Newfoundland.

The major predators of juvenile and adult Sea Scallops include invertebrates such as Rock Crab (Nadeau and Cliche 1998), American Lobster, sea stars (Nadeau and Cliche 1998), Moon Snails, burrowing anemones and finfish such as Atlantic Cod, American Plaice and wolffish. Sculpins and Winter Flounder have also been identified as predators, especially of scallops that have been damaged by fishing gear. Boring worms and sponges often attack older Sea Scallops. Stokesbury and Himmelman (1996) examined the movements of Sea Scallops through a tagging study and found that scallop movement did reduce predation rate and that it was weakly correlated with the abundance of Rock Crab.

Two-year old cultured and wild Sea Scallops from the Gulf of St. Lawrence were compared in terms of escape response, morphometric indices and biochemical indices (Lafrance *et al.* 2003). Cultured scallops had larger somatic tissues and higher muscle energetic contents than the wild ones, perhaps reflecting the more favourable temperatures and better food supply during

suspension culture. However, when confronted with the starfish predator *Asterias rubens*, the cultured scallops appeared more vulnerable to predation than the wild scallops. Cultured scallops responded to the predator presence with a greater number of valve claps, longer clapping period and faster recuperation after clapping, but the wild scallops had stronger shells and exhibited more intense escape responses (higher clapping rate) to the starfish.

Relation to Man

Important Canadian commercial Sea Scallop fisheries occur on Georges Bank, in the Bay of Fundy, on the Scotian Shelf, in the Gulf of St. Lawrence and on St. Pierre Bank. Inshore harvesting in Newfoundland occurs along the south coast (Placentia Bay, Fortune Bay and St. Mary's Bay) and on the west coast in Port au Port Bay. Depending on location, scallops attain size for exploitation by ages 4 to 7 (DFO 1996e). Recreational Sea Scallop harvesting conducted by SCUBA diving occurs around the coast of insular Newfoundland.

Overexploitation of natural stocks sparked renewed interest in eastern Canadian scallop aquaculture in the 1980s. A pilot-scale facility to produce juvenile Sea Scallops associated with the Marine Sciences Research Laboratory of Memorial University of Newfoundland showed consistent and reliable results as recently as the late 1990s, but it has since been closed (Couturier *et al.* 1995). Aquaculture sites in Newfoundland for the Sea Scallop have been located in Port au Port Bay, Bay of Islands, Fortune Bay, Notre Dame Bay and Connaigre Bay. The landed value of Sea Scallops in Newfoundland and Labrador during 2006 was approximately $871,093 (517 mt), down from 2005 at $3,854,134 (2,176 mt) (DFO 2007a).

Young-Lai and Aiken (1986) discussed the potential for Sea Scallop aquaculture. They concluded that technology developed in Japan could be adapted for Newfoundland, but that necessary modifications would be locality-specific. The commercial feasibility of polyculture of Sea Scallops with Atlantic Salmon (*Salmo salar*) was recently examined in northeastern Maine (Parsons *et al.* 2002). Growth and survival data indicated the potential for supplemental income, diversification of the salmon aquaculture industry and feasibility of culturing scallops at sites adjacent to salmon operations. Penney and Mills (2000) published a bioeconomic analysis of *P. magellanicus* aquaculture production in Newfoundland.

Laboratory experiments and modelling were conducted to estimate the potential spatial and temporal effects of water-based drilling mud on Sea Scallop growth around hypothetical exploratory well sites (Gordon *et al.* 2001). The authors concluded that the potential effects in shallow, well mixed zones with high dispersion appear to be negligible. The greatest potential effects were predicted for slope areas where depths exceeded 100 m and dispersion was low.

3.3.13 Short-Finned Squid (*Illex illecebrosus*)

Distribution

In the northwestern Atlantic Ocean, Short-Finned Squid occur from Greenland to Florida and are most concentrated in the region between the Gulf of St. Lawrence/Newfoundland and Cape Hatteras (Stephen 1982). Abundance and distribution of this squid species are highly variable, both intra- and inter-annually (Black *et al.* 1987; Rowell 1989). Canadian Shelf squid samples

were discriminated from Canadian Slope squid samples based on twenty-four morphometric body and beak characters (Martinez *et al.* 2002).

Generally, during April to June, young squid (3 to 6 months) migrate from the Slope Water beyond the edge of the continental shelf onto the Grand Banks, the Scotian Shelf, Georges Bank and the mid-Atlantic Bight shelf area in order to feed. In June, the greatest concentrations of squid occur along the edges of the Scotian Shelf and Georges Bank and along the southwestern edge of the Grand Banks. The schooling squid are predominantly male early in the shoreward migration, but by fall, females are predominant. During July to September, the Short-Finned Squid distribution extends to cover large areas of the continental shelf, sometimes including the Gulf of St. Lawrence (Rowell 1989). Squid abundance generally peaks during September and then falls dramatically in October and November as the larger, maturing squid leave the shelf. Their distribution in the fall decreases to that observed in early summer. The inshore and offshore distributions of this squid species appear to be strongly affected by environmental conditions, particularly water temperature (Coelho 1985). Evidence suggests that squid concentrations are highest when bottom temperatures exceed 6 °C.

Results of tagging studies indicate that the Short-Finned Squid head southwest upon leaving the shelf area. It is believed that the adults migrate to a spawning area near Cape Hatteras or even further south over the Blake Plateau off the southeastern U.S. (Dawe and Hendrickson 1998). Since 1979, research surveys have reported the annual occurrence of larvae and juveniles extending more than 1,500 km along the Gulf Stream frontal zone and shoreward in the Slope Water off the edge of the continental shelf. It appears that the Gulf Stream might act as a transporter of the various squid stages northeastward from the spawning grounds. Trites (1983) concluded that based on Gulf Stream dynamics, neutrally buoyant squid larvae and small juveniles could be rapidly transported as far as 100 km/day northeastward toward the Grand Bank.

Life Cycle

Spawning and Fertilization: Considering that they die after spawning, Short-Finned Squid probably live no more than 12 to 18 months (Cargnelli *et al.* 1999c). Mating may occur well before spawning given that the spermatophores are implanted in the female mantle cavity. Spawning females create large, clear, almost neutrally buoyant egg masses by releasing a gel-like substance with the fertilized eggs. O'Dor and Balch (1985) indicated that the gel appears to function as a buoyancy mechanism which prevents the eggs from sinking. They theorized that if spawning is indeed pelagic, then common oceanographic situations where water density increases with depth could allow the egg masses to be suspended in the mesopelagic zone (depth range of 200 to 1,000 m), possibly at the pycnocline. Suspension in this zone would provide temperatures adequate for embryonic development.

The presence of spermatophore bundles, attached either to the inner wall of the mantle cavity or at the base of the gills near the oviducal gland, indicated that 31% of the Stage 5 female squid collected during a May 2000 survey had mated (Hendrickson 2004). This survey was conducted on the continental shelf of the east coast of the U.S. from George's Bank to North Carolina (~ 35.5 to 41.5 °N). Most of the mated females were caught in the portion of the survey area

extending from 36 to 39 °N (Mid-Atlantic Bight) at depths ranging from 113 to 377 m. Since squid are thought to spawn shortly after mating, this region is thought to be a spawning area of this squid species. This area was characterized by surface temperatures of 13.4 to 20.1 °C and bottom temperatures of 11.4 to 20.3 °C.

Fertilized Eggs and Larvae: The egg mass can be up to 1 m in diameter and contain as many as 100,000 eggs, 1 mm in diameter. The egg-mass buoyancy, rate of temperature equilibration and terminal velocity affect the sinking rate of the egg-mass. Depending on water temperature, hatching generally occurs about 2 weeks after fertilization. O'Dor *et al.* (1982) demonstrated that embryonic development failed at temperatures below 12.5 °C and that the development rate was twice as fast at 21 °C than at 12.5 °C.

Hatching times for squid are variable. Dawe and Beck (1997) back calculated hatching dates from the examination of squid statoliths taken from Newfoundland waters in 1990. They found that hatching had occurred between December and June, but that peak hatching occurred during the March to May period. Those squid that had hatched later exhibited higher growth rates and more advanced reproductive state. Samples of Short-Finned Squid were collected during a stratified random bottom trawl survey in May 2000 on the continental shelf of the east coast of the U.S. from George's Bank to North Carolina (~ 35.5 to 41.5 °N) (Hendrickson 2004). The population consisted of a predominant winter cohort of maturing and mature squid (hatched during October to February, with a peak in January) and a spring cohort of juveniles (hatched during February and March, with a peak in March).

The hatching larvae are approximately the same size as the eggs. These larvae have been found in nature at water temperatures ranging from 5 to 20 °C and most abundantly at water temperatures exceeding 16.5 °C and salinities exceeding 34 ppt (Cargnelli *et al.* 1999c). The larvae are most abundant in late January to February in the nutrient rich waters of the Gulf Stream/Slope Water zone and the warmer water (> 13 °C) above the thermocline (i.e., variable depths). Larval squid develop into juveniles with 6 mm long mantles and adult features. The larval proboscis has split to form the two tentacles and the eight arms have lengthened. The larvae are prey for larger planktivores and they, in turn, feed on small zooplankton.

Juveniles and Adults: The juvenile Short-Finned Squid live in the Gulf Stream frontal zone and the Slope Water off the edge of the continental shelf until they reach about 10 mm mantle length. At this time, they move into the adult feeding areas on the shelf. Growth rates of juveniles are poorly known, but it is documented that adult squid add roughly 1.5 mm in mantle length per day, reaching 25 to 30 cm mantle length by October-November. It is not known what fraction of the Short-Finned Squid population resides in continental slope waters deeper than the survey strata (366 m) or in oceanic waters (Dawe and Hendrickson 1998). Juvenile Short-Finned Squid have been caught in water temperatures ranging from 5 to > 16 °C and in high salinity water (> 33 ppt) (Cargnelli *et al.* 1999c). Adults appear to have an even wider tolerance of water temperature (< 0 to > 27 °C). They tend to be found in waters with salinities exceeding 30 ppt (Cargnelli *et al.* 1999c).

Mahon *et al.* (1998) identified the Short-Finned Squid as part of the "southern deepwater" assemblage (outside the slope waters from Laurentian Channel to Cape Hatteras), which occurs

at waters deeper than 200 m. In their analysis of environmental effects on the survey catches of *Illex illecebrosus* in the northwest Atlantic Ocean between 1967 and 1994, Brodziak and Hendrickson (1999) found that catches of Short-Finned Squid were relatively low and associations with environmental factors were inconsistent. Depth had a weak effect on the magnitude of juvenile and adult catches, with the ratio of juvenile to adult catches decreasing with depth. Catches of Short-Finned Squid were lowest at night, the diel effects being more pronounced for juveniles than for adults. Bottom and surface water temperatures had a variable influence on *I. illecebrosus* catches.

Through use of a multiple regression model, the effects of variation in the ocean environment on abundance of northern Short-Finned Squid in the northwest Atlantic Ocean were investigated (Colbourne *et al.* 2002; Dawe *et al.* 2000). The analyses indicated that squid abundance was positively related to a favourable oceanographic regime associated with a negative North Atlantic Oscillation index (weak winter northwesterly winds), high water temperatures off Newfoundland and a southward shift in the position of the Gulf Stream and the boundary between the shelf waters and the offshore slope waters. In addition, increased meandering of the Gulf Stream appears to promote increased abundance, possibly through enhanced shoreward transport of squid.

Dawe *et al.* (1998a; 2007) found strong correlations between the squid abundance index for Subareas 3+4 and numerous environmental indices, particularly between Subarea 3 and the North Atlantic Oscillation, the Gulf Stream Front and the Shelf-Slope Front. These strong correlations suggest that winter-spring conditions during the early oceanic phase of the life cycle are important in regulating recruitment. The progeny of the winter spawning group in southern U.S. waters are advected to northern waters in synchrony with the springtime productivity peak. This strategy is highly adaptive in that environmental conditions which promote strong year classes also favour population expansion through expedient advection of young stages and a suitable oceanographic regime in the northern-most area, thereby assuring sufficiently rapid growth and maturation to support the long spawning migration and completion of the life cycle.

Perez *et al.* (1996) investigated a method of growth increment used to reconstruct individual squid growth histories and study growth patterns in wild populations. They evaluated growth increments deposited in the dorsal surface of the gladius and compared these to depositions on the statoliths. They concluded that the daily growth increments on the gladius are enumerable. Critical transitions in early life histories of Short-Finned Squid were reconstructed from gladius growth by Perez and O'Dor (2000). They associated gladius length ranges and some life history stages including the paralarval stage, to a shift from macroplanktonic to micronektonic habitats and transition from the Gulf Stream to Slope Water. Hendrickson (2004) indicated that female Short-Finned Squid from U.S. waters reach maturity and spawn at smaller sizes and younger ages than females from Newfoundland waters. These results suggest that females from the Mid-Atlantic Bight may exhibit faster rates of growth and maturation and possibly a shorter lifespan than their Newfoundland counterparts.

The juveniles and adults tend to remain near the bottom during the day and move upwards in the water column at night. Juveniles feed most heavily on small crustaceans such as euphausiids. As the squid grow into adulthood, their diet expands to include larger crustaceans, fish and even

other squid. Dawe *et al.* (1997) reported on the fish prey spectrum of more than 17,000 Short-Finned Squid taken at 11 coastal Newfoundland localities during 1980-1993. Most of the prey, based on the otoliths found in just over 8,000 squid, were young-of-the-year Atlantic Cod, but also included adult Capelin, juvenile Sand Lance, Arctic Cod, Atlantic Herring, redfish and hake. Garrison (2000) used bottom trawl survey data to look at spatial and dietary overlap in the Georges Bank groundfish community of which Short-Finned Squid was a component. Short-Finned Squid (10-30 cm length) were most abundant in the assemblages sampled in the offshore habitats of southern New England and south of Georges Bank during both spring and autumn.

Analysis of stomach contents of almost one thousand Short-Finned Squid taken on the continental slope of Nova Scotia and New England during August to November indicated that crustaceans (euphausiids), fish (unidentified) and squid were the most important components of their diet, accounting for approximately 65% by weight. There are indications that feeding is most intense at night (Vinogradov and Noskov 1979).

The Short-Finned Squid has been identified as a prey item for various fish, marine mammals and birds. Some of these predators include tunas, swordfish, haddock, cod, pollock, sharks, Pilot Whales, dolphins, shearwaters, fulmars, gannets and gulls. This squid species has been found to be the almost exclusive diet of the Long-Finned Pilot Whale in Newfoundland waters (Squires 1957). Paz *et al.* (1993) reported that cod feeding on the Flemish Cap in 1989 and 1990 included Short-Finned Squid in their diet. Overholtz *et al.* (2000) provided estimates of consumption by 12 piscivorous fish species on the continental shelf off the eastern U.S. and southeastern Canada between 1977 and 1997. One of the prey species considered was *I. illecebrosus*. The authors concluded that the estimated consumption of squid by the predatory fish appears to equal or exceed squid landings in most of the years examined.

Relation to Man

Fisheries for Short-Finned Squid throughout the northwest Atlantic Ocean likely target a common single stock (Dawe and Hendrickson 1998). The Newfoundland inshore squid fishery in the northern part of the squid distribution area typically extends from July to November, with peak catches occurring between August and October. The fishery in the southern part of the distribution area generally peaks in May or June (Dawe 1999). The large catches in Subareas 3+4 (Newfoundland and Nova Scotia area) in the late 1970s did not appear to adversely affect the squid resource to the south in Subareas 5+6.

During 1976-1981, annual Subarea (SA) 3+4 landings averaged approximately 80,000 mt, peaking at 162,000 mt in 1979. However, during 1983-1997, the annual SA 3+4 commercial landings averaged only slightly over 4,000 mt, peaking at 15,485 mt in 1997 (Rivard *et al.* 1998). Hendrickson (1999) examined the trends in relative fishing mortality rates in relation to spawner biomass levels during 1983-1997. She found that mean weights of squid caught during 1982 surveys had declined following the period of high landings in Subareas 3+4 during 1976-1981. Hendrickson *et al.* (2004) also reported that during 2003, the relative abundance and biomass indices for *I. illecebrosus* from the Canadian Divisions 4VWX July survey were well below the 1982-2002 average, indicating a state of relatively low productivity for the Subareas 3+4 stock component.

3.3.14 Long-Finned Squid (*Loligo pealeii*)

Distribution

In the northwest Atlantic Ocean, the Long-Finned Squid ranges from Canadian waters south to the Gulf of Venezuela (Stephen 1982; Dawe *et al.* 2007). They also occur around Newfoundland and on the Scotian Shelf, but in low abundance compared to the southern end of its range (Black *et al.* 1987). Dawe *et al.* (1990) described a major extension of the geographic range of the Long-Finned Squid based on its occurrence in Newfoundland inshore trap samples in the autumn of 1986. Dawe *et al.* (1990) found that biological data from the Newfoundland samples compared to samples from Nova Scotia indicated that Long-Finned Squid spawn in Nova Scotia, but not Newfoundland waters.

North of Cape Hatteras, the Long-Finned Squid undertake seasonal migrations to avoid cold waters with bottom temperatures less than 8 °C and to occupy favourable spawning grounds close to juvenile nursery areas in coastal waters. In early winter, this squid species migrates offshore to avoid the autumn cooling of coastal waters. Submarine canyons and areas along the edge of the continental shelf at depths of 100 to 250 m have warmer water temperatures (9 to 12 °C) during the winter and provide suitable habitat for this species. In the spring, Long-Finned Squid migrate inshore to the continental shelf and coastal waters (< 100 m) where they spawn and feed. The Long-Finned Squid grows very rapidly and completes its life cycle in less than one year (Brodziak and Macy 1996; Brodziak 1998).

Life Cycle

Spawning and Fertilization: Long-Finned Squid spawn in the spring through summer in shallow water, primarily between Cape Cod and Cape Hatteras. A single viable egg mop of *L. pealei* was found at Bay Bulls, Newfoundland in August 2000, which was the first evidence of spawning by this squid species at the northern limit of its geographic range of distribution (Dawe *et al.* 2001; 2002). Because many cephalopods are thought to be semelparous, questions remain as to whether some cephalopods spawn multiple times. Maxwell *et al.* (1998) discussed evidence for multiple spawning by Long-Finned Squid in captivity over a period of several weeks. Brodziak and Macy (1996) reported that Long-Finned Squid are able to spawn year round inshore. Most eggs appear to be spawned around May, followed by hatching in July (Summers 1971).

Griswold and Prezioso (1981) described *in situ* observations on reproductive behaviour of Long-Finned Squid along the coast of Rhode Island. During the summer, individuals and egg masses are common in this area. The Long-Finned Squid were particularly numerous at night, occurring singly or in small, loosely formed schools. They observed a large egg mass (50 to 60 cm in diameter) attached to the side of a small boulder in 6 m of water and at a temperature of 14.5 to 15.0 °C. Surrounding substrate consisted of sand and mud with sparse algal clusters. The egg masses normally seen in this area were 12 to 15 cm in diameter. Griswold and Prezioso (1981) reported that numerous breeding pairs approached the egg mass and stopped about 3 m from the mass, forming a semi-circle around the egg mass. In turn, each pair approached the cluster of finger-like egg capsules and the females deposited more fertilized eggs.

Copulation supposedly occurs just before egg deposition. The male cements bundles of spermatophores into the mantle cavity of the female and as each egg capsule (50 to 80 mm long and 10 mm in diameter; 150-200 eggs) passes out through the oviduct, the sperm penetrate it (Cargnelli *et al.* 1999d). Each female lays 20 to 30 capsules. The capsules are laid on the bottom in clusters 50 to 60 cm wide. Egg masses are often found attached to rocks and small boulders on sand/mud substrates and various algae. The demersal eggs are generally laid at depths < 50 m.

Egg mass guarding by solitary males and breeding pairs has been reported. King *et al.* (1999; 2003) conducted experiments to determine whether male *Loligo pealeii* use sensory cues provided by egg mops to regulate agonistic behaviour. The authors manipulated the egg mops to provide differing sensory stimuli (i.e., tactile, water-borne and visual). Results indicated that tactile stimulation caused the greatest increase in agonistic behaviour and that visual stimuli maintained the level of agonistic behaviour between egg mop touches. Water-borne stimuli alone did not cause any increase in agonistic behaviour. Buresch *et al.* (2004) provided evidence that the salient chemical factor that causes the agonistic behaviour originates in the female reproductive tract.

Fertilized Eggs and Larvae: Embryonic development in Long-Finned Squid takes approximately 10 to 27 days, depending on water temperature (12 to 23 °C). Optimal salinity for embryonic development ranges between 30 and 32 ppt. Macy (1995) reported that New England Long-Finned Squid spawn throughout the year. From the examination of 457 squid, he determined that 36% hatched during March-May, 27% during June-August, 28% during September-November and only 7% during December-February. The larvae are pelagic in the near surface waters and are known as paralarvae (Cargnelli *et al.* 1999d). These larvae occur at temperatures of 10 to 26 °C and salinities of 31.5 to 34 ppt.

Juveniles and Adults: Newly hatched individuals actively maintain position at the surface under illumination. Vecchione (1981) collected planktonic juveniles over the Middle Atlantic Bight off New Jersey and Virginia during spring, summer and fall. Specimens were absent during winter collections. Peak abundances occurred during late summer and most were caught at night. Vecchione (1981) found that hatching was continuous during the warm months throughout the study area. The planktonic juveniles were taken in waters with a salinity range of 31.5 to 34.0 ppt. Juvenile Long-Finned Squid have been found in water temperatures ranging from 8 to 23 °C (Cargnelli *et al.* 1999d).

There are two basic life stages prior to attaining sexual maturity: 1) juvenile and 2) subadult. Generally, the juvenile stage lasts 1 to 2 months in the upper 10 m of the water column at depths ranging between 50 and 150 m. The subadult stage follows the juvenile stage, normally overwintering in deeper waters along the continental shelf before undergoing final maturation. Subadults occur at depths intermediate between those of juveniles and adults (Cargnelli *et al.* 1999d). Pre-recruits have been taken at a variety of depths (surface waters to 130 m, depending on season and location). Adult Long-Finned Squid are primarily demersal, while juveniles migrate vertically upward in the water column at night to avoid predators or to find prey. The shift to a demersal lifestyle occurs at about 45 mm.

Garrison (2000) studied spatial assemblages and dietary guilds of various groundfish species in the Georges Bank area. During the spring, small and medium (10 to 30 cm) Long-Finned Squid were caught primarily offshore, but accounted for only 2.5% of the total biomass taken in that area. During autumn, the same sized individuals appeared more widespread in distribution, particularly the small ones (10 to 15 cm). Small Long-Finned Squid co-dominated with butterfish in terms of percentage of total biomass caught in the offshore area. With respect to the dietary guilds, Long-Finned Squid accounted for 16%, by weight, of the diets of Atlantic Cod and Summer Flounder during the autumn, but its contribution to diets in the spring was negligible.

Based on Long-Finned Squid samples collected during August-November in 1974 and 1975 on the continental slope of Nova Scotia and New England, squid (26.2%) and unidentified fish (49.2%) dominated the diet on a percent by weight basis. Decapods (9.8%) and unidentified crustaceans (8.4%) ranked a distant third and fourth, respectively. During this study more than 1,300 squid were examined. The diets of larger squid (16 to 30 cm mantle length) were dominated more by fish and squid compared to the smaller squid (8 to 15 cm mantle length) (Vinogradov and Noskov 1979). Other studies have also found that fish tend to dominate the diet of adult Long-Finned Squid (Maurer and Bowman 1985).

Gut content analyses have shown that the diet of Long-Finned Squid differs between inshore spawning/nursery areas and offshore winter grounds (Macy 1982). In New England, Long-Finned Squid collected inshore during May to November and offshore during the winter were shown to consume crustaceans more frequently than either fish or squid. However, fish were eaten by a wider size range and were consumed more frequently inshore. The data suggested that Long-Finned Squid are highly opportunistic predators.

Juvenile and adult Long-Finned Squid are preyed upon by many pelagic and demersal fish species (mackerel, cod, haddock, pollock, hake, dogfish and flounder), marine mammals (Long-Finned Pilot Whale and Common Dolphin) and diving birds. Gannon *et al.* (1997) reported that Long-Finned Squid was the most important prey item of thirty Long-Finned Pilot Whales (*Globicephala melas*) captured off the northeastern U.S. Overholtz *et al.* (2000) provided estimates of consumption by twelve piscivorous fishes on the continental shelf off the eastern U.S. and southeastern Canada between 1977 and 1997. One of the prey species considered was *L. pealeii*. The authors concluded that the estimated consumption of squid by the predatory fish appears to equal or exceed squid landings in most of the years examined.

Relation to Man

The Long-Finned Squid remains an important commercial resource in the northwestern Atlantic. This species, along with other cephalopod species, is often used in biomedical neuronal research.

There has been work carried out concerning the feasibility of culturing loliginid squid species. Vidal *et al.* (2002) investigated the various factors that affect the survival of *Loligo opalescens* hatchlings, specifically diet type, water quality and current speed. Although this work was conducted on a California species of squid, the knowledge gained is probably transferable to other species, especially loliginid species.

3.3.15 Arctic Squid (*Gonatus fabricii*)

Distribution

This arcto-boreal circumpolar squid is distributed in offshore Arctic and subarctic waters of the northern North Atlantic, extending as far as Newfoundland and Labrador (Roper *et al.* 1984; Nesis 2001). Stephen (1982) indicates that the distribution extends to areas on the Scotian Shelf and Georges Bank. Vecchione and Pohle (2002) reported the capture of *Gonatus fabricii* off Nova Scotia during mid-water pelagic trawls in the late 1980s. The depth range of this oceanic species is typically between surface waters and 500 m. While the adults are common to mid-column waters of the Arctic and subarctic, juveniles inhabit the surface waters of the northwest Atlantic, including waters around Newfoundland and Labrador. The general biology of this species is not as well known as the Short-Finned or Long-Finned Squid.

Life Cycle

Statolith shape, morphometry and microstructure have been investigated as indicators of ontogenetic shifts and ecological lifestyle specifics in *G. fabricii* (Arkhipkin and Bjørke 2000; Arkhipkin 2003).

Spawning and Fertilization: Spawning appears to extend from April to December, peaking in late May and June. Kristensen (1984) found that male *G. fabricii* collected off the coast of Greenland in autumn were in spawning readiness. Nesis (2001) stated that this squid typically spawns on the bottom or in mid-water at depths exceeding 500 m.

Fertilized Eggs and Larvae: Kristensen (1983; 1984) suggested benthic deposition of fertilized eggs, possibly as deep as 400 to 500 m. Mangold (1987) hypothesized that this squid species releases its egg masses in the surface layers of the water column. During their work off the Norwegian coast, Bjørke *et al.* (1997) caught egg masses in a pelagic trawl fishing the column over the 600 to 1,100 m depth range during July. The corresponding bottom depth range was 1,160 to 2,660 m. Essentially all of the egg masses were caught where water temperatures were less than 0 °C and it is likely that the water salinity was high (> 18 ppt). Mature squid were often caught along with the egg masses. The number of eggs deposited may be as high as 10,000. Bjørke *et al.* (1997) described the eggs as large (4 to 6 mm in diameter) and encased in a gelatinous mass. Falcon *et al.* (2000) reported the capture of *G. fabricii* paralarvae from the mid-North Atlantic Ocean during the spring and summer months. None were found in the samples collected during fall and winter.

Juveniles and Adults: Juveniles are approximately 3 mm at hatching. Kristensen (1983) stated that the juvenile stage persists until an approximate length of 30 mm is attained. Juveniles are often found in the uppermost 80 m of the water column over depths of 200 to 500 m, but they have been caught at depths up to 1,000 m. The adults occupy greater depths. Bjørke *et al.* (1997) found that young *G. fabricii* with mantle lengths less than 50 mm were common in the upper 60 m of the water column during May surveys in Norwegian waters. Juveniles and adults are believed to migrate vertically upwards at night. Bjørke (1995) found *G. fabricii* distributed throughout the Nordic Seas. He observed mainly juveniles in the upper 30 m of the water column and adults at depths greater than 300 m. Dalpadado *et al.* (1998a) reported the highest densities of *G. fabricii* in the upper 30 m of an Atlantic/Arctic water mass during a summer

survey in the Nordic Seas. The salinity was at least 34 ppt in this part of the column. Both the juveniles and adults prefer high salinity waters (> 18 ppt).

Adult *G. fabricii* (Dalley, E.L., DFO, pers. comm.) have often been caught in shrimp trawls over soft bottoms. Since 1994 during plankton and nekton surveys on the northeast Newfoundland Shelf and Grand Banks. Substantial amounts of *G. fabricii* have been caught. In 1998, the overall catch of this squid was about one-third that of the previous year, but the distribution was similar. They were mainly over the central northern portion of the Northeast Shelf, with a less dense concentration over the Southeast Shoal area. Between 1994 and 1998, the catch rate of this squid was highest over the inner shelf off Southern Labrador (Dalley *et al.* 1999).

Juveniles feed on copepods, euphausiids, amphipods, pteropods and chaetognaths. As these squid grow, fish and other squid become the most important component of their diet (Nesis 2001). *G. fabricii* is a prey for various marine mammals (Hooded Seals, Harp Seals, Northern Bottlenose Whale and Sperm Whale) (Lick and Piatkowski 1998; Folkow and Blix 1999; Bjørke 2001; Hooker *et al.* 2001; Santos *et al.* 2002; Simon *et al.* 2003; Haug *et al.* 2004), marine birds (fulmars and Thick-Billed Murre chicks) (Lydersen *et al.* 1989; Barrett *et al.* 1997; Garthe *et al.* 2004), gadoids, Greenland Halibut (Dawe *et al.* 1998b; Michalsen and Nedreaas 1998; Hovde *et al.* 2002) and redfish (Roper *et al.* 1984).

Relation to Man

This squid is an important prey species for many commercially important finfish species.

3.3.16 North Atlantic Octopus (*Bathypolypus arcticus*)

Distribution

Bathypolypus arcticus is an arcto-boreal species occurring throughout the North Atlantic Ocean. In the northwestern Atlantic Ocean, the North Atlantic Octopus is distributed along the continental slope from Greenland to the Straits of Florida, including the Gulf of St. Lawrence and the Bay of Fundy (Nesis 2001). This benthic species has a broad depth distribution that ranges from < 20 m to over 1,000 m. It is often caught over a sand/mud substrate (Roper *et al.* 1984; Humes and Voight 1997). Nesis (2001) reported that specimens caught in the Siberian Arctic at depths ranging from 180 to 362 m were over substrates consisting of mud/stone, stone/sponge and sand. Grassle *et al.* (1975) photographed a *B. arcticus* individual partially buried in a silt/clay substrate at 1,300 m off the southern U.S. coast.

Life Cycle

Spawning and Fertilization: This octopus appears to breed throughout the year (Roper *et al.* 1984; Nesis 2001). There is no clear evidence to indicate that the reproductive cycle of *B. arcticus* is seasonal (O'Dor and Macalaster 1983). All records of spawning were made in summer or early autumn suggesting that egg laying might be associated with rising water temperatures. It appears that this octopus may move to rocky substrates to spawn. Wood *et al.* (1998) made the first detailed observations of mating, brooding and embryonic development by *B. arcticus*. Eighteen specimens collected during scallop surveys in the Bay of Fundy were

maintained under laboratory conditions. They observed the transfer of 1 or 2 spermatophores from the male octopus to the female mantle. Two females laid and brooded viable eggs.

Fertilized Eggs: Nesis (2001) indicated that spawned eggs within capsules are usually attached singly to some overhanging surface near the ocean bottom and are then brooded by the female. O'Dor and Macalaster (1983) reported that a brooding female with 50 eggs was incidentally taken from a 100 m depth on St. Pierre Bank off southern Newfoundland. The substrate at this catch location consisted primarily of rock. A captive female was observed brooding her eggs for almost a year (August to July) in an area where water temperature ranged from 3 to 10 °C. Wood *et al.* (1998) reported that brooding and embryological development in the laboratory lasted just over one year at water temperatures of 7.3 to 7.8 °C. Brooding females ate very little during the brooding process.

Juveniles and Adults: *B. arcticus* hatchlings typically weigh approximately 0.15 g and look like miniature adults (i.e., a pelagic larval stage is bypassed). The weights of hatchlings in the laboratory (Wood *et al.* 1998) ranged from 0.21 to 0.28 g. The female octopus dies soon after hatching (Wood *et al.* 1998). The juveniles will immediately grip the substrate and they will not swim unless irritated. Juvenile North Atlantic Octopus caught in the Siberian Arctic had mantle lengths ranging from 8 to 18 mm (Nesis 2001).

The maximum mantle length of this small octopod is about 10 cm, but the average length is around 6 cm. Individuals in the Atlantic Ocean rarely exceed 50 mm mantle length (Nesis 2001). Adults from the Siberian Arctic ranged from 28 to 57 mm mantle length (Nesis 2001). Adult weight rarely exceeds 200 g (O'Dor and Macalaster 1983). This species is eurybathic (10 to 1,000 m depth, but most common at 200 to 600 m) and eurythermic (3 to 11 °C) (Wood *et al.* 1998; Roper *et al.* 1984). A typical 70 g female appears to require 3 to 4 years to complete her life cycle stages of embryonic development, growth, gametogenesis and egg brooding (O'Dor and Macalaster 1983).

This opportunistic feeder is known to forage on animals typically inhabiting soft substrates (e.g., brittle stars, various small crustaceans, sipunculids, polychaetes, bivalves, gastropods) (O'Dor and Macalaster 1983). They are also known to scavenge dead animals. Various bottom fishes (e.g., cod, haddock, hake) are the primary predators of the North Atlantic Octopus (Macalaster 1981; O'Dor and Macalaster 1983; Roper *et al.* 1984).

Relation to Man
This octopus is not fished commercially.

3.4 ANNELIDA (Polychaetes)

General Information
Of the approximately 9000 species of annelids, more than 8000 are polychaetes. Polychaetes comprise a substantial component of benthic marine communities associated with all types of substrates. There are a large number of cosmopolitan polychaete species, which exhibit high adaptability and a wide variety of life histories that can change under different ecological conditions (Gosner 1979).

Based on polychaete distributions, Pocklington and Tremblay (1987) identified three faunal zones within the coastal region of the northwest Atlantic Ocean between Hudson Strait and Cape Hatteras. Habitat off Newfoundland and Labrador are included in two of these zones; the Labrador faunal zone and the Acadian faunal zone. The Labrador zone includes the inshore and offshore Labrador coast to the Strait of Belle Isle as well as waters on the Grand Banks deeper than 50 m. Most of the Acadian zone areas have depths less than 50 m and include shallow coastal waters, estuaries and bays around the Avalon Peninsula (Conception Bay, Trinity Bay, Placentia Bay). Numerous polychaete species occur around Newfoundland and Labrador and species and genera discussed in this profile occur here (Catto *et al.* 1999; Hooper 1997).

3.4.1 Clam Worms/Sandworms (*Nereis* spp.)

Distribution

Nereis species of the western North Atlantic are distributed from the Arctic south to the mid-U.S. eastern coast. They can occur from the upper intertidal zone to the deep subtidal (Gosner 1979). Barrie (1979) found *Nereis pelagica* at Hopedale and Nain, Labrador within a depth range of 11 to 20 m. Fine sand dominated the sediments at Nain and a mix of sand and gravel characterized the substrates at Hopedale.

Life Cycle (*N. virens*)

Spawning and Fertilization: The sexes are separate in this polychaete species. Gametogenesis in both sexes is complete by April or May (Creaser and Clifford 1982; Wilson and Ruff 1988) and individuals die after they reproduce. Water temperatures in excess of 7 to 8 °C appear to be necessary for spawning to occur in sandworms. During their study of the life history of an intertidal population of *N. virens* on the south shore of the St. Lawrence Estuary, Desrosiers *et al.* (1994) found that spawning occurred primarily from late April to early June. They observed that the males released their sperm and this triggered oocyte release by the females. Creaser and Clifford (1982) found that during both years of their study in a Maine estuary, spawning occurred about 4 days after the full moon during the period of spring tides. Fecundity, seemingly dependant on the size of the female, ranges from 50,000 to 1.3 million eggs. In laboratory experimentation using *N. virens* from the White Sea, successful fertilization occurred in a salinity range of 22 to 34 ppt (Ushakova and Sarantchova 2004). Lewis *et al.* (2002) reported that maximum fertilization success occurs at water temperatures ranging from 15 to 18 °C. Some nereids are strong swimmers and emerge in breeding swarms at different times of the year.

Fertilized Eggs and Larvae: Fertilized eggs are extruded onto the surface of the muddy substrate and embryonic development occurs on or near the sediment surface (Desrosiers *et al.* 1994). Planktonic embryos are not apparent. Trochophore larvae enter the plankton, but only for a very short time (< 1 day) (Wilson and Ruff 1988). Desrosiers *et al.* (1994) observed both benthic and pelagic larval development, followed by settlement on the upper intertidal zone. In laboratory experimentation using *N. virens* from the White Sea, successful early development of the fertilized eggs occurred in the salinity range of 22 to 34 ppt (Ushakova and Sarantchova 2004). However, trochophore and nectochaete larvae were more euryhaline, successfully developing in a wider salinity range (14 to 45 ppt). The highest rate of metamorphosis occurred at a temperature of 23 °C and at salinities > 14 ppt.

Lewis *et al.* (2003) observed that the reproduction of *N. virens* occurs at a time of year when seawater temperatures are lower than the optimum temperatures for fertilization and larval development and at a time when seawater temperatures are rising. Their study in England assessed the possible role of intra-specific competitive interactions between settling *N. virens* post-larvae as a selective pressure for early reproduction. The results suggested that pre-emptive competition between the settling post-larvae did form a strong selective pressure for breeding early at a time of year when temperatures are below the optimum for fertilization and development.

Nereis sp. larvae have been found to be strongly associated with "marine snow" (Shanks and del Carmen 1997). Samples from this study were taken from the upper 5 m of the water column.

Juveniles and Adults: Juveniles are benthic about 12 days after fertilization and crawl into the intertidal zone after approximately 16 weeks (Wilson and Ruff 1988). Desrosiers *et al.* (1994) observed the approximately 3 year old juveniles migrating down slope to join the adult *N. virens*. Miron *et al.* (1991) concluded that juveniles and adults compete for burrow space rather than for food. The lifespan of this polychaete has been estimated at 7 years (Desrosiers *et al.* 1994).

Caron *et al.* (1993) also reported on their investigations of *N. virens* in the St. Lawrence Estuary. In north and northeast facing intertidal flats, they found the highest densities of juveniles in the higher tidal levels where sediment organic matter content was greatest and the lower densities of adults in the sandy lower intertidal area where sediment organic matter content was low. On the flats facing southwest, juveniles were densest in the gravel sediment of the lower intertidal zone, while the adults were most apparent in the upper intertidal. They concluded that the inter-population variability of this polychaete was dependent on numerous hydrodynamic effects (larval spatial patterns and segregation of sediment organic matter) and thickness of the colonisable sediment layer. They also concluded that adult-juvenile interaction was important in the regulation of this population.

Miron and Desrosiers (1990) found that the density of *N. virens* was highest in the uppermost level of intertidal flats located in the lower St. Lawrence Estuary. They also reported that densities increased with increasing organic matter content in the sediment. Higher densities were associated with higher gravel content, while increasing sand content was associated with lower *N. virens* density. Sexually mature sandworms were found only at the lower intertidal level supporting the belief that larvae of this species are recruited in the upper intertidal zone and juveniles migrate down shore. Spatial distribution patterns did not differ between spring and fall.

The salinity tolerance of this euryhaline animal varies from 1 ppt to full salinity. The surface and bottom salinity ranges in an estuary in Maine where *N. virens* were found were 17 to 29 ppt and 24 to 29 ppt, respectively while surface and bottom water temperatures ranged from 1 to 15 ° C and 1 to 14 °C, respectively (Creaser and Clifford 1982). Although its non-lethal range is wide, preferred temperatures of *N. virens* range from 11 to 20 °C (Wilson and Ruff 1988). In the Aber Estuary, North Wales, Williams (2003) found *Nereis* spp. in areas where temperature, salinity and pH ranges were 11 to 13 °C, 1.4 to 15.2 ppt and 8.0 to 8.5, respectively, while the substrate consisted primarily of a sand/silt mixture.

Although these active polychaetes burrow in a variety of substrates where they form sandy tubes glued together with mucus (Gosner 1979), muddy substrate is preferred. Highest densities are found in the lower intertidal zone. Winter migration by non-reproductive adults may be a mechanism to find more suitable benthic habitat (Wilson and Ruff 1988). In the Aber Estuary, Williams (2003) found *Nereis* spp. occupying the sediments from the surface to 60 cm sediment depth. According to Hooper (1997), *Nereis* polychaetes are key organisms of the biota assemblages in Newfoundland and Labrador termed "seagrass bed" habitat which is characterized by sand to fine gravel substrates and shallow estuarine conditions, including low exposure to wave energy (Hooper 1997). Examples of locations around the coast of Newfoundland where "sea grass" habitat occurs includes St. Paul's Bay, Piccadilly Harbour in Port au Port Bay, Mortier Bay on the Burin Peninsula, North Harbour in St. Mary's Bay and Bellevue in Trinity Bay (Hooper 1997).

Caron *et al.* (1996) studied the spatial overlap between the polychaetes *N. virens* and *Nephtys caeca* in two intertidal estuarine environments in the lower St. Lawrence Estuary. The greatest overlap was between the adult stages of each species, particularly in the lower area of the intertidal zone (> 25 cm) where organic matter content was lower. The juvenile stages of each species generally inhabited the organic rich upper portions of the intertidal sediments (0 to 12 cm).

Generally, sandworms are strong predators on many kinds of invertebrates, including amphipods and other sandworms. They feed by extending a portion of their bodies from burrow openings. The burrows tend to be in the upper 10 cm of mudflats. Last (2003) reported that out-of-burrow activity in *N. virens* is restricted to the hours of darkness and that the activity away from the burrow entrance is concentrated in the period just after the onset of darkness when feeding is most intense. The food prospecting (burrowing) by *N. virens* possibly decreases in the autumn and then picks up again in late winter (Last and Olive 2004). The authors speculated that the autumn cessation may maximize the fitness of this spring breeding polychaete by reducing risk during gamete maturation. They suggested that the late winter resurgence of activity might permit animals that are physiologically incompetent to spawn an opportunity to build up metabolic reserves. They also feed on algae and will scavenge if the opportunity arises, so they are omnivorous. Olivier *et al.* (1993) studied the spatial and temporal variations in the feeding of *N. virens* inhabiting tidal flats in the St. Lawrence Estuary. They found that the diet varied with habitat characteristics and polychaete age. Juveniles were primarily deposit feeders, while adult polychaetes were almost exclusively carnivorous. *Nereis diversicolor* was observed feeding on juvenile bivalves in the Wadden Sea (Hiddink *et al.* 2002). Caron *et al.* (2004) described and compared the feeding activities of *N. virens* and *N. caeca* in relation to several environmental factors. These two polychaetes exhibited a high degree of dietary overlap, especially at the adult stage. However, they appear to exhibit different feeding responses to environmental stimuli, favouring their co-occurrence.

N. diversicolor was found to significantly increase the decay of fresh and aged *Fucus serratus* detritus in sediment, thereby directly and indirectly affecting microbial activities (Kristensen and Mikkelsen 2003). The detritus is redistributed by the burrowing and feeding activities of this polychaete. In the absence of irrigated burrows, a larger fraction of partly degraded detritus might remain undegraded and be buried permanently in the sediments.

N. virens are common prey for bottom-feeding finfish and decapod crustaceans (Gosner 1979). Various gull (Ambrose 1986) and tern species as well as the Common Eider are known to feed on these polychaetes, particularly the spent ones (Wilson and Ruff 1988). Shorebirds such as plovers and sandpipers are known to feed on *N. virens* in the St. Lawrence Estuary (Michaud and Ferron 1990). *N. virens* is generally found in the same environment as Softshell Clams (*Mya arenaria*) and the nemertean *Cerebratulus lacteus* in Atlantic Canada. Bourque *et al.* (2001b) conducted aquaria experiments to evaluate the relationship between these three species. This study revealed an apparent migratory response of *N. virens* to the presence of the nemertean, perhaps because the nemertean is a potential predator.

Relation to Man

Sandworms have been harvested in Maine for years to be used as bait in recreational saltwater fishing. Europeans have being conducting commercial aquaculture of these polychaetes since the 1980s for the same reason (Olive 1999). *N. virens* is a valuable research organism for man due to the ease associated with culturing it in the laboratory. It is also used as an indicator species in environmental studies (Wilson and Ruff 1988). Other species of *Nereis* have also been used as bioindicators (Pérez *et al.* 2004).

Ray (2000) conducted research in Maine which demonstrated that diverse, complex infaunal assemblages, including *N. virens*, can be established on mudflats constructed of dredged materials. Within three years of construction, the infaunal assemblages of one mudflat resembled those of natural intertidal flats with respect to species composition, assemblage structure, diversity and abundance.

Addition of *N. diversicolor* to organic rich sediments surrounding a marine fish farm in Denmark resulted in increased mineralization rates after a two-month period (Heilskov and Holmer 2003). The work provided evidence for fauna-mediated shifting in the mineralization pathway towards more exodized conditions and increased aerobic mineralization in bioturbated sediments.

3.4.2 Lugworm (*Arenicola marina*)

Distribution

Arenicola marina occurs from the Arctic to Cape Cod on soft bottoms in both the intertidal (Oug 2001) and subtidal zones. These animals produce U-shaped burrows with openings on both ends surrounded by coiled castings. This polychaete species filter feeds on fine particulate matter carried by bottom currents through their burrows (Gosner 1979). *A. marina* typically burrows to a depth of 15 cm.

General Information

Gilbert *et al.* (1984) reported *A. marina* occurring on the intertidal flats located near Nain, Labrador. Their burrows were most evident in gravel/sand substrates distributed throughout the intertidal flats. Densities of this polychaete on the flats ranged from 2 to 11 m^2.

Study of benthic community structure and sediment processes on an intertidal flat in the Netherlands indicated that the biomass of surface deposit feeders, such as *A. marina*, was highest where bottom shear stress was moderate and the sediment consisted primarily of sand with little

mud (Herman *et al.* 2001). Aitken *et al.* (1988) investigated intertidal flat communities in Baffin Island and found that *A. marina* inhabited the medium/coarse sand flats slightly seaward of the bivalve *Macoma balthica*. Other suspension feeding bivalves in the community included *Mya truncata* and *Hiatella arctica*.

According to Hooper (1997), *Arenicola* polychaetes are key organisms of the biota assemblages in Newfoundland and Labrador "seagrass bed" habitat characterized by sand to fine gravel substrates and shallow estuarine conditions, including low exposure to wave energy (Hooper 1997). Examples of locations around the coast of Newfoundland where "sea grass" habitat occurs includes St. Paul's Bay, Piccadilly Harbour in Port au Port Bay, Mortier Bay on the Burin Peninsula, North Harbour in St. Mary's Bay and Bellevue in Trinity Bay (Hooper 1997).

Watson *et al.* (2000) analyzed thirteen years of data relating to the annual epidemic spawning period of a Scottish population of *A. marina*. They investigated the possibility of predicting the synchronous spawning of this Lugworm from environmental parameters. This Lugworm population exhibited discrete 4 to 5 day spawning periods sometime between mid-October and mid-November. Correlation of spawning times with weather patterns showed that mean daily air pressures were significantly higher during spawning than from September to November as a whole. They also found evidence which suggested that a reduction in sea temperature was needed prior to spawning. Daily rainfall and wind speed were also lower during the spawning period. Watson *et al.* (2000) emphasized that the cues they observed may not necessarily apply to other populations of this widely distributed polychaete and that the evolutionary significance of autumn spawning is still unknown. Lewis *et al.* (2002) determined the temperature limits and optimum temperature for fertilization of *A. marina*. Fertilization success of *A. marina* was significantly influenced by temperature, with maximum success at 15 to 18 °C. The ambient seawater temperature at the time of natural spawning by this Lugworm is about 10 °C, meaning that it is spawning at the lower limit for maximum fertilization. Salinity and exposure of *A. marina* sperm to sub-zero temperatures also influenced fertilization success, but only at levels that would not be experienced by this Lugworm under natural conditions at time of spawning. *A. marina* appears to wait as late as possible to maximize adult fecundity and survival.

As an inhabitant of the littoral zone, *A. marina* lives under characteristic conditions of sharp fluctuations in temperature, salinity, oxygen supply and duration of exposure on the surface. Morphological and biochemical adaptations facilitate the survival of these animals in their burrows under such variable conditions (Alyakrinskaya 2003).

In a North Sea intertidal sand flat, Reise *et al.* (2001) compared a Lugworm population during a summer immediately after a severe winter with that of a summer before and a summer later to determine whether a severe winter affected distribution patterns of adult and juvenile Lugworms and how summer recruits responded to spatial changes of adult abundance. Juveniles normally overwintered in subtidal channels and then colonized the upper tidal zone above the range of the adults. Reise *et al.* (2001) found that after a severe winter, the population size of the adult Lugworms was halved and the juveniles were therefore more widely distributed (i.e., into the lower tidal area which was typically colonized by adults). However, this disturbance effect by the severe winter on the Lugworm population was brief and did not carry over into the next year.

The thermal tolerance window of *A. marina* to the environmental temperature regime was studied in two intertidal populations, one from the North Sea (boreal) and the other from the White Sea (subpolar) (Sommer and Pörtner 2002). Lugworms of the White Sea population were adapted to lower mean annual temperatures than those of the North Sea population (4 vs. 10 °C). The White Sea Lugworms exhibited an overall higher capacity of aerobic energy production with cold adaptation.

Arenicola sp. larvae have been found to be strongly associated with "marine snow" (Shanks and del Carmen 1997). Samples from this study were taken from the upper 5 m of the water column. Andresen and Kristensen (2002) examined the distribution of bacteria and chlorophyll *a* in sediment around and within *A. marina* while feeding on sandy sediment in a shallow bay in Denmark. They discussed the importance of each in the diet of this Lugworm throughout an annual cycle. Flach (2003) discussed the effects of macro-infauna, including *A. marina*, on the recruitment success of bivalves in shallow soft bottom areas on the Swedish coast. Hiddink *et al.* (2002) also reported the predation by *A. marina* on bivalve spat.

3.4.3 Terebellid Worms (*Amphitrite* spp.)

Amphitrite johnstoni is the most common boreal species of this genus and ranges as far south as New Jersey. It is commonly found intertidally on mud flats and eelgrass beds at salinities as low as 15 ppt.

In soft substrates, terebellid worms lie buried in the substrate with only their heads exposed. Elsewhere they can be found attached to the undersides of rocks. Terebellids typify the deposit feeding method used by polychaetes. Their tentacles are grooved and coated with mucus and can be extended over the substrate in all directions from the mouth of the burrow (Gosner 1979).

Hooper (1997) included *Amphitrite* polychaetes as key genera of the biota assemblage associated with the Newfoundland and Labrador "kelp bed" habitat, characterized as having hard substrates (bedrock and boulders), high salinity, low temperatures and moderate to high exposure to wave energy. Most of the coast of Newfoundland and Labrador typifies this habitat type (Hooper 1997).

3.4.4 Hard Tube Worms (*Spirorbis* spp.)

Spirorbis species in the western North Atlantic occur from the Arctic to Long Island from the intertidal to deep water. Substrates to which they attach include rockweed (Teo and Ryland 1995), rocks and shells (Gosner 1979).

Spirorbis spirorbis typically breed during the winter (January-February) (Jennings and Hanna 1988). Development of embryo to the trochophore larval stage occurs within the adult polychaete and the larvae eventually free themselves and enter the free-swimming phase that lasts for 12 to 36 hours. The larvae eventually settle and attach themselves by a calcareous secretion. Within one hour of settlement, the permanent calcareous tube is being formed. Dick *et al.* (1998) reported that *Spirorbis* spp. occurred as epibionts on the exposed outer surfaces of male Tanner Crab (*Chionoecetes bairdi*) in Alaska.

Daly (1978a) described the annual life cycle and reproductive cycle of *S. spirorbis* in detail. He studied a population in England living intertidally on an algae, *Fucus serratus*. These polychaetes are hermaphrodites and the embryos are incubated as a string within the parent's tube. Oocyte output was positively correlated with individual size (Daly 1978b). Those that survive the winter produce a succession of broods from May through to September in the year following settlement. As breeding season progresses, the time between spawning and larval release decreases to an observed period of about 20 days. The synchrony within the population of both spawning and egg release increases during the breeding season even though the events do not appear to be synchronized with any obvious environmental variable.

In many marine invertebrates, the failure to fertilize eggs or larval death during early development in the plankton, constitutes a major source of mortality. However, in *S. spirorbis*, losses up to the time of larval release from the parent's tube are almost negligible (Daly 1978b). Given the short duration of the free-swimming larval stage, losses up to the time of settlement may also be relatively small.

The combined effect of salinity and temperature on *S. spirorbis* larvae from the White Sea was studied in laboratory experiments (Ushakova 2003). He found that *S. spirorbis* larvae distributed throughout the upper 20 m of the water column were resistant to salinities as low as 10 ppt. Highest survivorship of *S. spirorbis* larvae was evident at temperatures less than 5 °C under all experimental salinity treatments. Under temperature treatments of 10 to 15 °C, the larval survivorship was restricted under all salinity scenarios. The highest number of successful larval attachments was evident at salinities of 25 to 30 ppt. The life-history patterns of tubeworms were summarized by Kupriyanova *et al.* (2001).

Hooper (1997) included *Spirorbis* polychaetes as key genera of the biota assemblage associated with the Newfoundland and Labrador "kelp bed" habitat characterized as having hard substrates (bedrock and boulders), high salinity, low temperatures and moderate to high exposure to wave energy. Much of the coast of Newfoundland and Labrador typifies this habitat type. Two *Spirorbis* species were identified by Barrie (1979) in sand dominated sediment samples collected at three locations in Labrador. They were collected within a depth range of 11 to 31 m.

Daly (1978a; b) found that *S. spirorbis* was common only in sheltered bays with intertidal pools and almost completely absent on rocky shores without pools, even when *F. serratus* was common. Most individuals are never exposed to air and, therefore *F. serratus* on higher rocks between the pools carried very few *S. spirorbis*. The maximum individual life span is generally about 16 months. Settlement of juveniles on the fronds of *F. serratus* begins in June and extends in decreasing intensity until October. Hamer and Walker (2001) demonstrated that settling spirorbid larvae appear to avoid air dried biofilms (e.g., emersed *F. serratus* fronds).

3.4.5 Red-lined Worms (*Nephtys spp.*)

Distribution

Species of this polychaete genus found in the western North Atlantic are distributed from the Arctic to various locations on the U.S. northeast coast. They are common in the intertidal zone, but also occur at greater depths in the subtidal. Barrie (1979) found juvenile *Nephtys* spp. at

various locations in Labrador. Collections were made in sandy substrates over a depth range of 4 to 60 m. Adults of five different species of *Nephtys* were also collected by Barrie (1979) at various locations in Labrador and in Conception Bay, Newfoundland. All areas had substrates dominated by sand and a depth range of 3 to 90 m.

Life Cycle

Pre-Juvenile: Spawning and external fertilization in *N. caeca* generally occurs in the spring (Caron *et al.* 1995) and larvae are typically present in the water column from May to July.

Juveniles and Adults: Caron *et al.* (1995) reported that larval settlement of an intertidal population of *N. caeca* in the lower St. Lawrence Estuary did not occur in the intertidal zone, suggesting subtidal larval recruitment. Densities of this polychaete were greater in sandy sediment compared to rich organic sediments (Caron *et al.* 1993). They concluded that inter-population variability of *N. caeca* is due mainly to sediment texture (i.e. hydrodynamical processes).

Gilbert *et al.* (1984) observed the presence of *N. caeca* in some of the intertidal flats investigated near Nain, Labrador. Although this species sometimes occurred in the same flats as *Arenicola marina*, it was typically found in less sandy substrates. Another species of *Nephtys* was also found in the subtidal region at depths up to 45 m.

Nephtys polychaetes have been described by Hooper (1997) as key organisms of the biota assemblage associated with "clam bed" habitats found around Newfoundland and Labrador. These habitats are generally characterized by fine to coarse sand/fine gravel substrates, full salinity and a range of water temperature and exposure (Hooper 1997).

Miron and Desrosiers (1990) found that the density of *N. caeca* was highest in the lower level of intertidal flats located in the lower St. Lawrence Estuary. They also reported that densities decreased with increasing organic matter content in the sediment during the spring, but this relationship was not obvious in the fall. In the spring, higher densities were associated with higher sand content while increasing gravel content was associated with lower *N. caeca* density. No such relationship was evident in the fall.

Their salinity tolerances vary from estuarine conditions to fully marine conditions. They are active predators on other invertebrates and typically burrow in sand or mud. Members of this genus are capable swimmers and emerge to swim in sexual swarms (Gosner 1979). Beukema *et al.* (2000) and Van der Meer *et al.* (2000) presented long-term observations (1970-1997) on the dynamics of three polychaete species living on tidal flats of the Wadden Sea, one being the predatory *Nephtys hombergii*. It appeared that *N. hombergii* abundance was most affected by temperature and weather conditions, whereas the abundances of its two prey polychaetes species were determined primarily by predator abundance and food supply.

Caron *et al.* (2004) described the feeding activity of *N. caeca* on the southern shore of the Lower St. Lawrence Estuary in relation to several environmental factors and related it to the feeding activity of another infaunal predatory polychaete, *N. virens*. Tides and storm events were shown

to affect the feeding behaviours of both polychaetes. The authors concluded that different behavioural feeding responses likely favour the occurrences of these two polychaetes in the same trophic environment.

In a study of community structure and intertidal zonation of the macrobenthos on a beach in Belgium, Degraer *et al.* (1999) found that the low intertidal zone (mean tidal level to the subtidal) species association was dominated by *N. cirrosa*. This low intertidal association also showed a strong affinity with the subtidal *N. cirrosa* species association. The sediments of the intertidal zone consisted primarily of fine sand. Van Hoey *et al.* (2004) described a *N. cirrosa* community occurring at a location on the Belgian continental shelf with well sorted sandy sediments. This community was characterized by low densities and diversity.

Relation to Man

Nephtys species are often used as bioindicator species in pollution monitoring (Ellis and Ronaldson 1988; Bustos-Baez and Frid 2003).

3.4.6 Fan Worm (*Myxicola infundibulum*)

This polychaete species occurs in the western North Atlantic from the Arctic to New York Bight and is usually found in the lower intertidal zone at the northern part of its range. They normally occur at depths of 1 to 20 m, but have been documented at depths as great as 500 m (Shumway *et al.* 1988). MacKay (1977) reported that the optimal water temperature range and salinity range for this polychaete is 8 to 10 °C and 30 to 33 ppt, respectively. Fan Worms feed on food particles suspended in the water column and are common fouling animals on pilings, buoys, etc. They are common in rock crevices and among other sessile animals (Gosner 1979).

Dean *et al.* (1987) indicated that July to February is the typical period of spawning, fertilization and development for this dioecious broadcast spawner. The males release their sperm first, followed by female oocyte release. The fertilized eggs adhere to the bottom and embryonic development occurs within hours. Within 10 to 15 days (at 10 to 15 ° C), the larvae complete their transition to benthic juveniles. Substrate irregularities, crevices, corners and small holes appear to be attractive to the settling larvae. Sexual maturity is reached in approximately 2 years.

Hooper (1997) highlighted Fan Worms (*Myxicola infundibulum*) as key organisms of the biota assemblage associated with the "scallop bed" habitats that he described as a marine coastal habitat type around Newfoundland and Labrador. Characteristics commonly associated with these habitats include sand/gravel/shell substrates and wide ranges of water temperature and exposure (Hooper 1997). Himmelman (1991) reported the occurrence of this polychaete in three types of subtidal region in the northern Gulf of St. Lawrence: 1) moderately exposed, medium-sloped bottom at 10 to 15 m; 2) exposed, gently sloping bedrock platform at 15 to 20 m and; 3) gently sloped sediment bottoms in areas of strong tidal current at 15 to 20 m.

During benthic photographic transects on Sea Scallop beds in the Gulf of Maine, Langton and Robinson (1990) found that *M. infundibulum* was one of three dominant megafaunal invertebrates. The other two were the Sea Scallop (*Placopecten magellanicus*) and a Burrowing

Sea Anemone (*Cerianthus borealis*). This association was found on gravel/sand substrates at depths of 56 to 84 m. Langton and Robinson (1990) concluded that *C. borealis* predated on polychaete and scallop larvae.

Relation to Man

M. infundibulum is an important species in medical neuronal research because it has a large central nerve cord which can be readily used in experimentation (Shumway *et al.* 1988).

3.5 ARTHROPODA

3.5.1 American Lobster (*Homarus americanus*)

General Distribution

The American Lobster ranges from southern Labrador (Strait of Belle Isle) to Cape Hatteras in North Carolina. Offshore populations occur along the outer edge of the continental shelf and upper slope (110-145 m) from the southern Scotian Shelf off Nova Scotia southwards to Virginia (Lawton and Lavalli 1995; DFO 1996f; Ennis *et al.* 1997). Generally, lobsters are continuously distributed around the island of Newfoundland and along the Strait of Belle Isle portion of the Labrador coast, occupying a narrow band of rocky bottom in a depth range of 2 to 40 m (Ennis 1984; DFO 2003a).

Life Cycle

Mating between male and female American Lobsters usually occurs immediately following the female's molting (or ecdysis) during the summer months. The hormonal regulation of molting is sensitive to exogenous cues such as temperature, photoperiodicity, salinity and food availability (Aiken and Waddy 1980).

Spawning and Fertilization: The male releases a spermatophore, which is stored in a receptacle on the underside of the female's body and is carried until she spawns the following year. Aiken and Waddy (1986) and Nelson *et al.* (1988) reported that spawning of nearshore lobster populations is normally regulated by seasonal seawater temperature, but that photoperiod can assume a regulatory role if the winter seawater temperature remains abnormally high (10 to 17 °C). During summer and autumn months, the eggs are pushed from the ovaries and fertilized externally (Aiken *et al.* 2004). Once extruded, the fertilized eggs are attached to long hairs on the female's pleopods. Lobster fecundity increases exponentially with female size, ranging from a few thousand to several tens of thousands of eggs.

Campbell (1986) and Karnofsky and Price (1989) reported that ovigerous females exhibit low shelter fidelity and pronounced local migration, possibly to maximize water temperatures and thereby quicken embryogenesis. Figler *et al.* (1998) also suggested that the frequent change in shelters by ovigerous females might be due to evictions by male lobsters.

Fertilized Eggs and Larvae: Development of fertilized eggs is strongly influenced by water temperature. Perkins (1972) found that in Maine, lobster development stops, or is barely discernible, once water temperatures fall to about 6 °C. Bottom temperatures normally remain

this low during November to May, but if they remain low for a longer period, hatching will be delayed.

The female carries the developing eggs until the following summer, when the pre-larvae hatch. They remain attached until they molt into the first larval stage (Stage I), within 24 hours of hatching (Charmantier *et al.* 1991). Hatching can occur over a wide range of temperatures during the May to July period on the Atlantic coast of North America (Ennis 1995). Hatching generally begins around 10 to 15 °C and is most intense at 20 °C (Hughes and Matthiessen 1962). The female then releases the first stage larvae by fanning her pleopods. Ennis (1975) reported that American Lobster larval release occurs most frequently at night, usually shortly after darkness, although batches of larvae are often released at different times of the day as well. The larvae may be released over a period ranging from a few days to a few weeks. There is normally a two-year period between mating and pre-larval hatch (i.e., a two-year reproductive cycle) (Ennis 1995).

The three distinct larval stages are planktonic and are typically found in the upper 2 to 3 m of the water column for a period ranging from 2 to 8 weeks (Hudon *et al.* 1986); however, diel vertical migration by Stage I lobster larvae can range from 15 to 30 m. Field studies have suggested that the maximum depth of vertical migration of decapod larvae is related to the depth of the thermocline (Harding *et al.* 1987). During this time, lobster larvae are largely passive drifters, so their gross movements are greatly controlled by the direction of the wind and water currents. Both are generally onshore during the regular time of larval release. Hudon and Fradette (1993) described the wind-induced advection of larval decapods, including lobster, into a bay of the Magdalen Islands in the southern Gulf of St. Lawrence. Potential sources of lobster larvae have been investigated in Nova Scotia by modeling larval drift (Drinkwater *et al.* 2001).

Larval lobster prefer uncontaminated water above a critical temperature (~ 10° C) and salinity (~ 20 ppt). Lobster larvae commence feeding immediately upon release from the female (Ennis 1995). Food availability (phytoplankton and zooplankton) is a very important factor, particularly to Stage I larvae.

The Stage I lobster larvae measure about 8 mm in total length. These larvae are typically concentrated at, or near, the water surface during the night and, depending on the light intensity, may be at surface or at greater depth during the day. The diel vertical migration by Stage I larvae to lower depths expose the larvae to other planktonic animals and plants, ensuring a rich food supply. It is believed that lobster larvae display raptorial feeding behaviour. Stage II larvae are typically about 9 mm long and are more physically developed than the Stage I larvae, but behaviourally, they are similar. Stage III larvae are larger again (~ 11 mm) and more physically developed. However, Stage III lobster larvae are less light sensitive and are therefore found more often in the near surface waters (Ennis 1995).

Metamorphosis to the post-larval stage occurs at the fourth molt. Time of development from the onset of Stage I to the post-larval stage depends on water temperatures. At 22 °C, development time can be as short as 11 days but, at 10 °C, it can take almost 8 weeks to attain the post-larval stage (Ennis 1995). Salinity also impacts larval development rates. At temperatures of 15 to 17.5 °C, a salinity range of 21 to 32 ppt does not appear to affect

developmental durations and survival of the larvae, but salinities outside of this range have a negative effect. Charmantier *et al.* (2001) conducted a review of the adaptations to salinity throughout the development in both *Homarus americanus* and *Homarus gammarus*. They reported that salinity tolerance varies throughout development, with the 50% lethal minimum salinity for larvae ranging from approximately 15 to 17 ppt. It has been estimated that an average of nearly 99% mortality occurs between the first larval stage and completion of the post-larval stage. The metamorphic post-larvae look like miniature adult lobster, are light-seeking (like the Stage III larvae) and are commonly found in the upper 1 m of the water column (Hudon *et al.* 1986). Despite their increased swimming ability, these post-larvae still use winds and currents as their primary mode of transport. As the molt into fifth stage approaches, light becomes a repellent and the metamorphic post-larvae begin to seek shelter in the benthic environment The post-larvae are strong swimmers and it is thought that they are able to make excursions to the sea bottom in order to detect suitable settlement substrate (Incze *et al.* 2000). Upon recognizing appropriate substrate, the post-larvae settle and become benthic juvenile lobster upon the molt into Stage V. Laboratory experiments have indicated that the post-larvae are capable of delaying the molt into fifth stage for a period of time, until suitable settlement substrate is found.

The extent to which post-larval settlement originates with eggs produced in the same area is unknown. Incze and Naimie (2000) examined potential distances between hatching and settlement locations for lobsters in the Gulf of Maine using a coupled physical-biological model. They found strong spatial differences for all hatch times examined (i.e., early, mid and late season). Their model also demonstrated that a strong diurnal coastal sea breeze could contribute substantially to inshore movement during the neustonic portion of the post-larval stage.

James-Pirri *et al.* (1998) reported that planktonic post-larvae exhibit as much as a 30% variation in carapace length (CL). Seasonal and inter-annual patterns in American Lobster larvae and post-larval stage size (mean CL), percent size increase at molt and growth rates were studied for a lobster population at the Magdalen Islands (Ouellet and Allard 2002). They found substantial size variability and concluded that the great range in size at age, which is reported for lobsters might originate during the conditions for growth and development (e.g., water temperature) of the larval stages.

Plankton sampling was conducted in Bonavista Bay, Newfoundland from May to September, at different depths and distances from shore (Ennis 1983a). A small number of Stage I lobster larvae were taken in surface samples collected during onshore wind conditions. Squires *et al.* (1997) conducted plankton tows within 20 m of shore at St. Chad's, Newfoundland during the May to September period. Water depth did not exceed 9 m. Only 27 specimens of Stage I larvae were collected during July and August.

Planktonic lobster larvae are prey to surface feeding fish and large zooplankton. Lavalli and Barshaw (1986) and Barshaw and Lavalli (1988) discussed the relationships between predation on post-larval lobsters by cunners and a crab and the substrate types used during settlement.

Juveniles: Settling post-larvae quickly find refugia in the substrate and remain essentially hidden for the first year of their benthic lives. James-Pirri *et al.* (1998) concluded that timing of settlement was more influential on the size attained by the end of the first growing season than

initial CL at time of settlement. However, based on study recapture rates, James-Pirri *et al.* (1998) provided the first evidence that size at settlement may be important to post-settlement success.

Settling post-larval lobsters typically prefer inshore habitat with gravel/cobble substrates (Palma *et al.* 1999) and kelp cover. During their study in the Gulf of Maine, Palma *et al.* (1999) observed a conspicuous lack of newly settled lobsters on adjacent finer sediment substrates. However, lobsters more than 1 year old were found on finer substrates. In terms of settlement depth, newly settled lobsters were found on collectors at 5 and 10 m, but not at 20 m. Lobsters more than 1 year old were found at all depths. Lobster settlement extended over the period from early August to early September. Compared to Rock Crab, lobsters settled at lower densities, but in specific habitats and over a narrower range of environmental conditions. The abundance and distribution of older individuals (1 year +) of both species were similar at all scales. Investigations in New Hampshire and Maine have indicated that adolescent *H. americanus* burrow in eelgrass beds, utilize eelgrass as an overwintering habitat and prefer eelgrass beds to bare mud (Short *et al.* 2001).

Through controlled laboratory experimentation, the effects of shelter availability and intra-specific density on the behaviour, survival and growth of Stage V American Lobsters over a 25-day period were studied (Paille *et al.* 2002). Lobsters exhibited higher shelter fidelity when fewer were available. Overall, the findings suggested that settling lobsters may interact, that the frequency and intensity of interaction may be modified by relative shelter availability and lobster density and that such interactions may contribute to determine a cohort's fate.

Work on the early benthic phase (EBP) of the European Lobster (*H. gammarus*) has also been done in an attempt to determine the preferred habitats for settlement (Linnane *et al.* 2001). They described the results of quantitative airlift suction sampling from cobble habitat in Norway, Ireland, U.K. and Italy. Depths of the sampling sites ranged from 6.5 to 17 m and the substrates underlying the cobble included sand, bedrock, muddy clay and shell-sand. In the 67 m^2 of cobble sampled, no EBP European Lobsters were found. It is possible that cobble habitat is not the preferred substrate for these animals.

Van der Meeren (2000) studied predation on hatchery reared European Lobsters (*H. gammarus*) released in the wild in southwestern Norway on rocky and sandy substrates in winter and summer. The released post-larval lobsters were 12 to 15 mm CL. While predation on these lobsters occurred on both the rocky and sandy substrates in summer, predation in winter occurred primarily in the sandy habitat. Most of the predation occurred within the first hours after release. Identified predators included wrasses, Atlantic Cod, sculpin and crabs.

Micro-wire tags were used to identify individual post-larval and fifth instar lobsters, *H. americanus*, that were released into the field in Rhode Island and then recaptured a week later (James-Pirri and Cobb 2000). The intention of this study was to examine the effect of lobster size at settlement and timing of settlement on survival. Larger post-larvae and fifth instars were recaptured significantly more frequently than their smaller counterparts. There was no difference in the recapture rate for those post-larvae that delayed settlement as compared to those that settled at the normal time. The authors concluded that differences in recapture rate could be

due to differential survival, but they might also be attributed to emigration and/or behavioural interactions.

Early benthic lobsters prefer warm water and are more tolerant of lower salinity than the planktonic stages. Charmantier *et al.* (2001) conducted a review of the adaptations to salinity throughout development of both *H. americanus* and *H. gammarus*. They reported that salinity tolerance varies throughout development, with the 50% lethal minimum salinity at approximately 12 ppt in post-larvae. Colbourne *et al.* (2002) presented a review and short description of environmental stock relationships for some marine invertebrate species in Newfoundland Shelf waters, including *H. americanus*. Analyses of the temperature landings lag suggested that warm conditions early in the life cycle are somehow favourable for early survival for lobster within the inshore environment of Newfoundland. Early benthic lobsters will find refuge in the smallest crevasses and in kelp beds. As the lobster grows, sheltering requirements and thus the substrate particle size preference, will change (Wahle and Steneck 1991; 1992).

The transition from planktonic to benthic life stage is the most dangerous period in the life cycle of the American Lobster. Upon settlement, their main predators are bottom-feeding fish including cunner, sculpin and White Hake, depending on geographical location (Hanson and Lanteigne 2000). Cobble substrates comprised of variable-sized rocks appear to protect newly-settled and small juveniles (< 100 mm) the most against predators (Hudon 1987). While most lobsters eaten by fish are less than 50 mm long, larger ones have been found in larger fish. Published studies attempting to detect consumption of American Lobsters by fishes in the natural habitat are rare and reports of consumption by fish species such as Atlantic Cod and flatfish are anecdotal at best.

The smallest lobsters observed outside of their shelters during laboratory studies were about 20 mm CL. Subsequent laboratory observations found that the early benthic lobsters (< 20 mm) use a combination of raptorial techniques (carried over from larval stages) and suspension feeding techniques to capture the plankton from the water (Lavalli and Barshaw 1989). These small lobsters appear to generate currents through their shelters by pleopod fanning. This plankton diet, supplemented by feeding on in-shelter organisms such as worms and amphipods, allows these vulnerable-sized lobsters to remain sheltered during the first year of their benthic life. As the juveniles grow, they are found outside of shelters more often, foraging for food and exploring the territory.

Larger juvenile lobsters (at least 100 mm) that are not yet sexually mature behave in many ways like the adults. Goldstein and Tlusty (2003) provided evidence to support the idea that the characteristics of the settlement substrate can have a dramatic impact on the rate of development of claw asymmetry with potential fitness consequences. They found that lobsters on shell substrate yielded significantly more asymmetrical claws than those on cobble, sand and plant.

A juvenile lobster monitoring program involving the collection of time series data relating to abundance and distribution of juvenile American Lobsters was undertaken at twenty-four intertidal sites in the Gulf of Maine between May and October, 1997 to 2000 (Ellis and Cowan 2001). It found that peak EBP (≤ 40 mm CL) lobster densities coincided with peak substrate

temperatures recorded *in situ* at low tide. Mean lobster CL was greater and EBP density lower in eelgrass habitat than in rocky habitat.

The natural diets of immature lobsters (12 to 73 mm CL range) in Newfoundland were investigated during June to November (Carter and Steele 1981; 1982). The most frequently occurring prey types were sea urchins, mussels, Rock Crab, polychaetes and brittle stars. Rock Crab, brittle stars and mussels were the dominant food item most frequently. Sainte-Marie and Chabot (2002) determined the natural diet of American Lobsters ranging in CL from 4 mm (instar V) to 112 mm (adult) by examining stomach contents of animals in the Magdalen Islands, Gulf of St. Lawrence. They found that the percentage total volume of stomach contents accounted for by bivalve and animal flesh decreased from the smallest lobsters (< 22.5 mm CL) to the largest lobsters (> 22.5 mm CL). The reverse trend was seen for Rock Crab as a food source. This study was the first to examine the natural diet of shelter-restricted juveniles (SRJs) (< 14.5 mm CL), which were thought to be principally suspension feeders and, to a lesser degree, browsers and ambush predators in or near their shelter. Rather than planktonic organisms, foraminiferans, crustacean meiofauna, macroalgal debris, bivalve flesh and animal flesh were found in the stomachs of the SRJs.

Cowan (1999) presented the results of a study in Maine that was intended to establish a method for repeated year-round sampling of the abundance of young-of-the-year and juvenile lobsters in the lower intertidal zone. Lobsters were sampled monthly between 1993 and 1997 by overturning rocks along transects running parallel to the water's edge 20 to 40 cm below mean low water (MLW). Two distinct size classes of lobsters, 3 to 15 mm CL and 16 to 40 mm CL, were consistently found along the transect. The highest average densities were found during May to November (up to 8 individuals per m^2). Cowan's preliminary results indicate that areas of the lower intertidal zone may serve as nursery areas for post-larval lobsters that settle and grow for several years.

Adults: Adulthood is reached within 5 to 8 years, depending largely on the water temperatures in the area (Lawton and Lavalli 1995). In Newfoundland waters, lobsters take 8 to 10 years from time of hatching to grow to 81 mm CL, at which size 50% of females become functionally mature and extrude eggs.

Larger juvenile and adult lobsters prefer substrates consisting of a combination of coarser sized particles (large cobble and boulder) and finer substrate that permits burrowing. Kelp beds are also beneficial to large juvenile and adult lobsters. Christian (1995) surveyed 1.2 hectares of substrate at Broad Cove, Newfoundland and identified more than 200 lobster shelters that occurred primarily in areas of the study area with boulder/bedrock substrate (> 70%) and substantial kelp cover. Only twenty-two shelters were identified in areas with a sand substrate component. Physical characteristics often associated with this habitat type include mixed substrates with suitable rocks for burrows, generally full salinity, a wide range of affecting currents, areas with relatively warm summer water temperatures and a full range of exposure to wave energy (Hooper 1997).

Rangeley and Lawton (1999) demonstrated the value of analyzing lobster distribution patterns at multiple spatial scales. They compared two cobble habitats; one in the southern Gulf of St.

Lawrence where the habitat patches were extremely complex, but fragmented and the other in the Gulf of Maine where habitat patches were large with low fragmentation. The lobster size distribution within each area were quite different despite both being cobble habitats.

Adult lobster life is similar to that of adolescents except for the array of physiological, ecological and behavioural events that are related to reproduction. Larger juvenile and adult lobsters are primarily nocturnal. Christian (1995) used ultrasonic telemetry to study the diel activity and nocturnal movements of large juvenile and adult lobster at a Newfoundland location. He found considerable intra- and inter-individual variability in numerous parameters including frequency of activity, maximum distance from shelter, total distance moved and shelter fidelity. Although determined largely by inference, the apparent reasons for variability in activity included feeding, territoriality and area familiarization. Activity levels in lobster are related to water temperatures. Christian (1995) found that the incidence of active nights increased substantially once water temperatures reached 7 to 8 °C. Jury and Watson (2000) estimate that lobsters can detect temperature changes perhaps as small as 0.15 ° C.

Large juvenile and adult lobsters feed primarily on benthic invertebrates including crabs, sea urchins (Himmelman and Steele 1971), mussels (Ojeda and Dearborn 1991), polychaetes, periwinkles and sea stars (Ennis 1973; Reddin 1973; Elner and Campbell 1987). Being opportunistic feeders, they will also scavenge fish carcasses (e.g., Capelin) when they are available. Ennis (1973) described a shift to a more calcium-rich diet during molting season (July to September). During this time, the proportions of sea stars, sea urchins and mussels in the diet increased. Crabs remained the primary prey item throughout the year. Moody and Steneck (1993) discussed the apparent functional dichotomy between large decapods, such as *H. americanus* and smaller ones like *Cancer irroratus*. Rock Crab are capable of a greater diversity of predatory shell opening tactics than the American Lobster.

Lobsters around Newfoundland do not tend to display any large scale migratory behaviour. They do exhibit small scale movements to slightly deeper waters in the fall/winter and back to shallower regions in spring/summer, probably in response to storm episodes and increased turbidity and seasonal changes in water temperature (Ennis 1983b; 1984). It appears that individual lobsters exhibit a relatively high degree of fidelity to an area, even to particular shelter use. Lobsters in Nova Scotia have been found to perform large-scale migrations between shallow and deep water areas due to the width of the continental shelf (Campbell and Stasko 1985; Pezzack and Duggan 1986; Campbell 1989; Tremblay *et al.* 1998). There have been instances of Nova Scotia lobsters moving in excess of 100 km during one migratory movement. Mature lobsters tend to migrate greater distances than immature ones (Campbell and Stasko 1986). Haakonsen and Anoruo (1994) argued that depth of displacement is a more reasonable measurement of lobster migration than horizontal distance traveled. The review paper by Haakonsen and Anoruo (1994) suggested two distinct lobster populations based on their ecological habitation and migratory behaviour; deep-sea lobster that migrate and coastal lobster that may move within a limited range. A method that uses metal contamination in lobster digestive glands as natural environmental tags has been developed in Atlantic Canada to trace lobster movements in the Inner Bay of Fundy (Chou *et al.* 2002a). The results of tagging over 42,000 American Lobsters in the southwestern Gulf of St. Lawrence between 1980 and 1997 and the subsequent recapture of more than 8,000 animals showed that there is little interaction

between American Lobsters from different fishing areas at the benthic level (Comeau and Savoie 2002).

American Lobsters also utilize estuarine habitats in certain areas, although the extent of this is poorly understood. Watson *et al.* (1999) conducted an ultrasonic tagging study involving more than 1,200 estuarine lobsters and they found that the lobsters tended to move into the warmer estuarine waters during the summer, probably to enhance growth rate. During low salinity periods, lobsters tended to move to areas of greater salinity. Jury *et al.* (1994) found that lobsters would move out of an area when salinities fell to less than 12 ppt. Charmantier *et al.* (2001) conducted a review of the adaptations to salinity throughout development in both *H. americanus* and *H. gammarus*. They reported that salinity tolerance varies throughout development, with the 50% lethal minimum salinity at approximately 10 ppt in adults. Moriyasu *et al.* (1999) reported that lobsters in Prince Edward Island appeared to be using the Bideford River Estuary to regenerate claws, after which they would move off into deeper water.

Relation to Man

The inshore lobster fishery in Newfoundland is prosecuted with traps, which are generally set at depths less than 15 to 20 m during spring to early summer (April to July). Specific season dates vary between locations. Landing statistics for the Newfoundland fishery began in 1874. In 1992, landings peaked at roughly 3200 t, but declined through the 1990s. In Newfoundland, data suggests that roughly 1900 t of lobster was landed in 2004, with an approximate value of $21 million (DFO 2006a). Recent years have brought increased landings in some, but not all, Lobster Fishing Areas (LFAs). Recruitment overfishing is believed to be a significant cause of the population declines. In the Lobster Management Plan 1998-2001, Fisheries and Oceans Canada stipulated a May 1998 increase in the minimum CL (to 82.5 mm CL) for retention of lobsters caught in the Newfoundland fishery. This measure was intended to increase egg production. The minimum legal CL remains at 82.5 mm. Other fishery conservation practices implemented in Newfoundland include; "no-take reserves" and the V-notching of ovigerous female lobsters, thereby excluding those females from the legal fishery. V-notching is the voluntary process of cutting a shallow notch into a specific portion of the tail of an ovigerous female. When a V-notched female is caught during the commercial fishery, it must be released. The V-notch is retained for up to two molts, thus protecting the sexually mature female from commercial harvest for several years. Low levels of lobster emigration from no-take reserves was indicated in the work by Rowe (2001), suggesting that no-take reserves might offer increased survival to lobsters and subsequent benefits to the fisheries.

Van der Meeren (2000) studied predation on hatchery reared European Lobsters (*H. gammarus*) released in the wild and concluded that survival of these small lobsters is probably highest if released during the winter in rocky habitat. Burton (2001) discussed the role of lobster (*Homarus* spp.) hatcheries in ranching, restoration and remediation programs.

The distribution of metals, PAHs and PCBs in American Lobsters has been used to assess marine environmental quality in the Bay of Fundy (Chou *et al.* 2003b). Compared to the Blue Mussel (*M. edulis*), *H. americanus* is a better bioindicator for monitoring because of its higher capacity for uptake and accumulation of contaminants.

3.5.2 Northern Shrimp (*Pandalus borealis*)

General Distribution/Habitat Preferences

Northern Shrimp, also known as pink shrimp, are most abundant north of 46 °N. In the northwest Atlantic Ocean, they occur from West Greenland (75 °N) southward to Georges Bank (42 °N) (Parsons and Fréchette 1989; Squires 1990). Water temperatures in areas of the northwest Atlantic Ocean, where the Northern Shrimp are most abundant range from 1 to 6 °C, sometimes restricting them to deep areas (i.e., > 180 m) (Koeller *et al.* 1996). Northern Shrimp appear to prefer areas with soft, mud, silt substrates but occasionally they will be found on sand and gravel/rock substrates (Williams 1984; DFO 1989a). These water temperature and substrate conditions occur throughout the Newfoundland-Labrador offshore area within a depth range of approximately 150 to 600 m, providing a vast area of suitable habitat (Orr *et al.* 2002; DFO 2006a; DFO 2003b; DFO 2000a).

Life Cycle

The Northern Shrimp is usually a protandric hermaphrodite, meaning that it first functions sexually as a male (one to several years), undergoes a brief transitional period known as sex inversion and spends the remainder of its life as a sexually mature female (secondary female) (DFO 1993b; DFO 2008a). There are some variations in its life history depending primarily on environmental temperatures. Some individuals mature directly as females from the juvenile phase and are called primary females. Primary females may occur in areas where temperatures remain high (6 to 14 °C) throughout the year. In the northwest Atlantic Ocean, primary females are rare. In areas where water temperatures remain below 0 °C, Northern Shrimp may remain males for their entire lives (Squires 1968).

Spawning, Egg Extrusion and Larvae: *Pandalus borealis* spawn once a year, generally around late June or early July. In eastern Canadian waters, shrimp eggs are extruded during late summer and fall and remain attached to the underside of the female's abdomen until hatching the following spring/summer. Fecundity has been shown to vary considerably according to individual size and area. In Atlantic Canada, the number of eggs per female usually ranges from 800 to 4,300 (Parsons and Tucker 1986). At water temperatures of 3 to 5 °C, Northern Shrimp females tend to be almost 100% ovigerous in autumn and spawn at least annually (Squires 1965). Ovigerous females may display seasonal horizontal migration to shallower warmer water areas in order to maximize the rate of embryonic development. The time between egg extrusion and hatching is temperature dependent, the shortest periods occurring in areas with higher temperatures (DFO 1993b). Larval hatching typically occurs sometime during the spring.

Upon hatching, larvae rise to near the surface where they start feeding on small plankton. After remaining planktonic for a few months, the larvae begin to move downwards in the water column and metamorphose to adult form (DFO 1993b). Berkeley (1930) found that larvae of a closely related shrimp off British Columbia hatched mainly in late March to early April, spent the early larval development time in deep water ($\geq$ 90 m) and then migrated to shallower water for final development. By winter, the young shrimp were ready to join the older individuals back in deeper water.

Storm and Pedersen (2003) studied larvae of an offshore population of *P. borealis* in West Greenland. Larvae were sampled in May, June and July at which time there was a decrease in abundances. The authors concluded that larval drift from hatch to settling covered distances of up to 500 km. Drift distances of shrimp larvae in the Barents Sea was estimated as high as 330 km (Pedersen *et al.* 2003).

Squires *et al.* (1997) collected Northern Shrimp larvae (Stage II zoea) during May to September plankton surveys in 9 m of water within 20 m of shore at St. Chad's, Newfoundland. The water temperature was 6 °C. Colbourne *et al.* (2002) presented a review and short description of environmental stock relationships for some marine invertebrate species in Newfoundland Shelf waters, including *P. borealis*. Based on statistical analyses, they concluded that cold years positively contribute to the survival of larvae and juveniles in the same year.

Juveniles and Adults: Most Northern Shrimp remain immature into the second year and then mature as males. Transition to the female form normally occurs during the early part of the fourth year, followed by ripening of the ovaries, mating and spawning (DFO 1993b). Females may spawn in one or more successive years and live for 5+ years. Northern Shrimp may function as males for several years before the inversion (Parsons and Fréchette 1989). Carapace lengths (CLs) of males and females reach 24 mm and 35 mm, respectively (Squires 1990).

Northern Shrimp must molt in order to grow. Growth slows and shedding of the outer shell becomes less frequent as the shrimp ages. The preferred temperature range for Northern Shrimp is 0 to 5 °C, temperatures below –1 °C are lethal (Koeller 1996). Colbourne and Orr (2003) presented the spatial distributions and abundance of Northern Shrimp in relation to their thermal habitat for NAFO Divisions 3LNO during spring surveys (1998-2003) and fall surveys (1995-2002). They found that the highest number of shrimp caught during spring surveys occurred within the 2 to 4 °C range and during the fall surveys, highest catches occurred where temperatures ranged from 1 to 3 °C. Very low numbers of shrimp were found in temperatures < 0 °C and > 4 °C during both spring and fall surveys. Preferred depth range is wide (50 to 500 m) and this species prefers fairly high salinities, although individuals have been reported in salinities as low as 23 ppt.

It is generally recognized that the average size of shrimp increases with depth except when the ovigerous females migrate to shallow water. Young males tend to be concentrated in shallow water, whereas females and transitionals are most abundant in deeper water (Parsons and Fréchette 1989).

Northern Shrimp exhibit diel vertical migration, spending time near the bottom during the day and moving upwards in the water column at night. During the day, Northern Shrimp feed on bottom items including worms, small crustaceans, detritus and marine plants. At night, the diet shifts to pelagic food items such as copepods and euphausiids. The migration consists mainly of males and smaller females (DFO 2008b). The Northern Shrimp prefers soft mud or silt substrates with a high organic content that provides a food source (DFO 2007b). Symbiotic associations between *P. borealis* and two anthozoan species were observed with remotely operated vehicles (ROVs) in temperate benthic (60 to 250 m) habitats off the Swedish west coast (Jonsson *et al.* 2001). It appeared that the shrimp were aggregating beneath the anthozoan tentacles for

protection against predators and to access food. Squires (1965) reported stomach contents that included crustacean fragments (euphausiids, amphipods and copepods), polychaetes and foraminiferans. Harvey and Morrier (2003) conducted laboratory feeding experiments on larvae of *P. borealis* fed with natural zooplankton. They found that the predation rate of Stage IV shrimp larvae increased with an increase in prey density. The predation rate of Stage II shrimp larvae increased with a temperature rise from 3 to 5 °C, but remained constant from 5 to 8 °C. The Stage II larvae ate primarily small prey, including copepod nauplii and eggs and nauplii of other invertebrates, while larger Stage IV larvae fed on larger prey as well as the previously mentioned smaller prey. Klages *et al.* (2002) provided experimental resu!ts suggesting that low frequency noises may be helpful to *P. borealis* for detecting food fall events, but only in the near field.

Northern Shrimp are known to be prey of Greenland Halibut (Vollen *et al.* 2004), Atlantic Halibut, other flatfish, cod, redfish and Harp Seals (Squires 1990; Lawson and Hobson 2000).

Relation to Man

The Northern Shrimp, *P. borealis*, is the only shrimp species of commercial importance in Atlantic Canada (Koeller *et al.* 1996). Commercial fisheries for Northern Shrimp have developed in several areas within its northwest Atlantic Ocean range. These areas include Davis Strait, deep-water channels off coastal Labrador, the Gulf of St. Lawrence, the Scotian Shelf and the Gulf of Maine. By 2005, about 101,150 t valued at about $154 million was landed in the Newfoundland Region (Government of Newfoundland and Labrador 2005). Canada is the largest producer of Northern Shrimp and the industry is worth well over $300 million (DFO 2000a).

Orr *et al.* (2005) reported on data collected in Divisions 3LNO each autumn since 1995. At least 90% of the Northern Shrimp biomass caught each year is found in 3L, mostly occurring within depths of 185-550 m. Since 1996, sampling was also conducted within St. Mary's, Conception, Trinity and Bonavista Bays. Most bay catches were made in Trinity and Bonavista Bays, but overall the bays contributed less than 9% to the total biomass estimates. Orr *et al.* (2005) described the Northern Shrimp resource in Divisions 3LNO as healthy with high abundances of both males and females.

Since 1984 catches of Northern Shrimp off the coast of Labrador and northeast Newfoundland (NAFO Division 0B, 2G and 3K) have increased steadily, peaking in 2004 at 117,500 mt (DFO 2006b). The fishery in early to mid 2000's was reported to be performing well with catch rates having no observable impact on the stock.

3.5.3 Krill (*Meganyctiphanes norvegica; Thysanoessa spp.*)

General Distribution

Krill (euphausiids), which are small shrimp-like crustaceans, comprise the most important macrozooplankton group in the pelagic ecosystem on the Canadian east coast continental shelf. They are the primary trophic link between small zooplankton and most fish species. They typically occur at depths exceeding 200 m and exhibit diurnal vertical migration to depths less than 50 m (DFO 1996g; 2000b). In the northwest Atlantic Ocean, *Meganyctiphanes norvegica* and *Thysanoessa* spp. (particularly *T. raschii* and *T. inermis*) are distributed in Newfoundland

and Canadian maritime waters south to Delaware Bay (Sameoto and Cochrane 1996). Kulka *et al.* (1982) discussed how euphausiid populations exhibit seasonal distributional variation due to variable hydrographic conditions. Matthews *et al.* (1999) discussed the physical oceanography of two separate European marine areas, as background to ecophysiological studies of *M. norvegica*. Their work provides evidence of the adaptability of this euphausiid to life under quite different oceanographic conditions.

Life Cycle

Spawning and Fertilization: *M. norvegica* releases eggs seasonally in multiple spawning events (Cuzin-Roudy 2000), but its breeding season varies with latitude. For example, this species exhibits winter-early spring breeding in the Mediterranean and the English Channel (Siegel 2000). Cuzin-Roudy *et al.* (2004) studied life cycle strategies of northern krill populations in Scandinavian and Scottish waters and found that spawning activity was limited to spring and summer despite the fact that trophic conditions still seemed favourable in early autumn. They noted that the phytoplankton community changed from a dominance of diatoms in spring to dinoflagellates in late summer, possibly triggering the autumn arrest of krill production. The synchronization in molting and spawning activity of northern krill and its effect on recruitment were analyzed by Tarling and Cuzin-Roudy (2003).

In the Canadian Maritimes, *M. norvegica* generally spawns during late June-early July, but spawning can extend into October. Berkes (1976) found no evidence of spring spawning by this species in the Gulf of St. Lawrence. He also reported that these euphausiids reach sexual maturity at age 1 and that male size at maturity is approximately 22 mm. Spawning by this species in the Passamaquoddy Bay area of the outer Bay of Fundy occurred from July to September (Hollingshead and Corey 1974). Tarling *et al.* (1999) found that spawning *M. norvegica* females were most evident in the upper depth interval (5 to 30 m) during late July-early August, perhaps to accelerate reproductive processes and also reduce the depth to which the eggs would sink before larval hatching. Fecundity of this species is difficult to estimate since they release their eggs directly into the water during multiple spawns.

Onset of spawning by *Thysanoessa* spp. off eastern Newfoundland has occurred in April (Jones 1969). Water temperatures at onset were approximately 1 to 2 °C and breeding continued until temperatures reached about 10 °C. In the Gulf of St. Lawrence, breeding season for the *Thysanoessa* species commonly begins around April. Breeding season for *T. inermis* continues into June, while it extends into September-October for *T. raschii* (Berkes 1976). Kulka and Corey (1978) found that the transfer of spermatophores to *T. inermis* females in Passamaquoddy Bay did not occur until mid-March. By the end of June, the percentage of females carrying spermatophores declined until none could be found by the end of July. Dalpadado and Skjoldal (1996) concluded that May to June was the main spawning time of *T. inermis* and *T. longicaudata* occurring in the Barents Sea, coinciding with the spring phytoplankton bloom. Astthorsson and Gislason (1997) also found that the primary spawning time of *T. inermis* and *T. longicaudata* coincided with the phytoplankton spring bloom. Kulka and Corey (1978) found that *T. inermis* in Passamaquoddy Bay spawned in May.

Fertilized Eggs and Larvae: The peak release time of planktonic fertilized eggs by *Thysanoessa* spp. generally occurs in late April-May in the Gulf of St. Lawrence. The developmental time between fertilization and hatching of the nauplius (earliest larval stage) is approximately 10 days. Hatching larvae, 5 to 8 mm in length, generally appear in the Gulf of St. Lawrence by August (Berkes 1976). Small numbers of early *Thysanoessa* spp. larvae were found in mid- to late summer in Passamaquoddy Bay (Kulka and Corey 1978). Immediate post-larval stages were first caught in July or August. It may take 3 to 4 months of development time between spawning and immediate post-larval stage. In Passamaquoddy Bay, eggs and non-feeding nauplii of *M. norvegica* were first caught during early July (Hollingshead and Corey 1974). Early larval development of this species in that area occurs from July to September.

Eggs and larvae of *T. raschii* were found in the northeastern part of the Laptev Sea, indicating that this euphausiid has a complete life cycle including maturation and reproduction in the Arctic Ocean (Timofeev 2000). The size variability of *T. raschii* embryos sampled in the Barents Sea appears to be caused by water temperature and salinity (Timofeev and Sklyar 2002). Embryo size was negatively correlated with temperature and positively correlated with salinity.

Juveniles and Adults: *M. norvegica* can live up to three years, but normally do not live past two years. *T. inermis* and *T. longicaudata* in the Barents Sea have life spans of 3 to 4 years and 2 years, respectively (Dalpadado and Skjoldal 1996). The size at maturity of *Thynsanoessa* species ranged from 10 to 18 mm in the Gulf of St. Lawrence. All were sexually mature by the end of their first year of life.

Many euphausiaceans live in great swarms that are generally 5 m or more thick. Brown *et al.* (1979) described daytime surface swarming by juvenile *M. norvegica* in the Bay of Fundy, while Barnes (1980) indicated that adults or near adults tend to dominate the surface swarms and developing juveniles tend to occupy the deeper water. Tarling *et al.* (1999) found that individuals of *M. norvegica* tended to remain in deep water at night (> 80 m), while the non-molting krill would migrate upwards, concentrating in the 50 to 80 m depth range. They offered "a cannibalism reduction mechanism" as an explanation for this segregation.

Observations during July and August submersible dives in the Gulf of Maine over a four-year period revealed interesting information about *M. norvegica* (Youngbluth *et al.* 1989). Swarms of this krill species were seen within the lower 15 m of the water column on the vast majority of the dives. They appeared to be foraging in the benthic boundary region. The mean densities of euphausiids in the epibenthic aggregations ranged from 100 to 2,800 individuals m^3 and the depths of the sampling transects ranged from 140 to 488 m. They normally observed only a few individuals in the upper mixed layer at night, indicating that perhaps only some krill of the bottom aggregation migrated upwards at night.

Simard *et al.* (1986a) observed similar concentrations of krill just above the bottom during their work in the St. Lawrence Estuary. They observed *Thysanoessa* spp. in addition to *M. norvegica*. At night, most of *T. raschii* and *M. norvegica* were below the 10 m pycnocline and during the day the upper level of the krill scattering layer (SL) was at about 50 m. *T. inermis* was also present in the krill SLs of the St. Lawrence Estuary and Gulf of St. Lawrence. The *T. raschii* SL was mainly composed of breeding adults of 1+ and 2+ age groups. They concluded that the krill

SLs in the St. Lawrence Estuary were not migrating to surface waters at night to feed on phytoplankton, but neither were they prevented from migrating vertically by the thermocline barrier. Simard *et al.* (1986b) found that the vertical distribution of euphausiids in the St. Lawrence Estuary during July was characterized by two principal modes, one at 75 m that was predominantly *T. raschii* and the other at 150 m which was predominantly *M. norvegica*.

Simard and Lavoie (1999) and Simard *et al.* (2002) reported on their survey of the rich krill aggregation at the head of the main channel of the estuary and Gulf of St. Lawrence during the summers of 1994 and 1995. The aggregation was deemed to be the richest one documented to date in the northwest Atlantic, explaining its traditional status as a whale feeding ground. The aggregations were composed of age 2+ individuals of *M. norvegica* and *T. raschii*. The krill were most concentrated during the daytime survey, at depths ranging from 25 to 75 m.

The aggregation and dispersion mechanisms of euphausiids (*M. norvegica* and *T. raschii*) at the head of the Laurentian Channel appear to be strongly influenced by a deepwater blocking process modulated by tidal cycle and freshwater runoff (Lavoie *et al.* 2000). In other words, circulation is the main factor controlling the abundance and distribution of krill in this area. Understanding krill aggregation dynamics is important given the trophic link with Baleen Whales and fish in the Saguenay-St. Lawrence Marine Park.

Saborowski *et al.* (2000) discussed the physiological response of northern krill, *M. norvegica*, to temperature gradients in the Kattegat channel off Denmark. This krill population is exposed to one of the most pronounced thermal gradients within its distributional range. During the summer, the temperature of the 140 m water column ranges between 4 and 6 °C in the deep water to 16 °C near the surface, resulting in the krill being exposed to temperature differences of 8 to 10 °C during diel vertical migration. During the day, essentially the entire krill population was found in the bottom portion of the water column, with at least 80% of the total catch occurring below 80 m. At night, krill migrated upwards and dispersed somewhat uniformly from 40 to 100 m. Tarling *et al.* (2000) developed an optimization model of diel vertical migration of this northern krill population and the sensitivity analyses indicated that the predicted diel vertical migration pattern was mainly driven by food and predation risk, with temperature effects on metabolic costs having a lesser effect. It has also been noted that female krill tend to migrate closer to the surface during diel vertical migration than males of equivalent size (Tarling 2003). It is speculated that the reason for this is that the greater demand for energy to fuel reproduction forces the females to undertake more risk.

Bergström and Strömberg (1997) studied the differences in the vertical migration pattern between *M. norvegica* and *T. raschii* caused by the presence of a thermocline and found that although *M. norvegica* would not migrate upwards through a thermocline at 50 to 60 m depth, *T. raschii* would. There was a temperature change of approximately 1.5 °C at the pycnocline.

The diel vertical migration of *M. norvegica* off Sweden was observed during a recent solar eclipse (Strömberg *et al.* 2002). They found that euphausiids reacted to a change in light intensity at midday, indicating that light is likely an important triggering mechanism for krill diel vertical migration. Liljebladh and Thomasson (2001) also discussed light as a triggering mechanism for krill diel vertical migration.

Herman *et al.* (1993) studied euphausiids in the Emerald and La Have Basins on the Scotian Shelf during the last week of September and first week of October. The La Have Basin contained *M. norvegica* adults below 160 m during the day and between 0 and 50 m at night. *T. inermis* adults were located between 70 and 100 m during the day, but at night they had moved up to the upper 50 m of water column, mostly in the 40 to 50 m depth range.

Kulka and Corey (1978) found *T. inermis* in Passamaquoddy Bay at depths greater than 45 m. Generally, more of these euphausiids were present during late summer and fall (July to November). The female to male ratio fluctuated, but tended to be highest during the spring and early summer, coinciding with the end of the breeding season. Throughout the sampling year, two separate year classes were present. Year class 0 appeared in late July-early August. Surface swarms in late summer consisted primarily of year class 0 individuals, while samples at greater depths were primarily year class 1.

Dalpadado and Skjoldal (1996) found that *T. inermis* were densest at depths between 400 and 500 m in the Barents Sea throughout the year and were generally most abundant during the winter (January to March). Nilssen *et. al* (1991) found that *Thysanoessa* spp. were most abundant in the Barents Sea during August-September immediately above the bottom (10 to 20 m above the bottom) at depths exceeding 250 m. There was also a concentration of these euphausiids in the upper 20 m of the water column at one of their stations. Bottom and upper column water temperatures were –0.1 °C and 0.55 °C, respectively.

During April in waters off northern Norway, Kaartvedt *et al.* (1993) located a layer of *T. inermis* at 150 to 200 m, about 100 m above the bottom. The region of their occurrence was an area of low light penetration. Above this layer were visually foraging predators of this euphausiid and below the layer was a concentration of another predator. Kaartvedt *et al* (1993) hypothesized that the euphausiids were actively avoiding predation and that in addition to water temperature and salinity, the optical properties of water appear important in delineating pelagic habitats.

<u>*Prey and Predators*</u>: Most euphausiids are filter feeders that use thoracic appendages to form a filtering apparatus (Barnes 1980). While *Thysanoessa* species are primarily phytoplankton feeders, *M. norvegica* is an omnivore (Sameoto and Cochrane 1996; Lass *et al.* 2001; Kaartvedt *et al.* 2002). Sameoto (1980) found that *M. norvegica* in the Gulf of St. Lawrence fed on copepods at their daytime depth of approximately 125 m and on phytoplankton and copepods at their nighttime depth of 75 m. Experimentation by Torgersen (2001) and Kaartvedt *et al.* (2002) showed that *M. norvegica* are visual predators on copepods. *T. raschii* is predominantly a filter-feeder, using raptorial methods to a much lesser degree than other krill species. No euphausiids are pure herbivores, but *T. raschii* is generally considered a species whose diet consists mostly of phytoplankton. Båmstedt and Karlson (1998) concluded that in Norwegian waters, *M. norvegica* ranked first in degree of carnivory on copepods, followed by the *T. inermis* and *T. longicaudata*. Berkes (1976) found that *Thysanoessa* spp. were omnivorous in the Gulf of St. Lawrence. There appeared to be less variability in the diet of *T. raschii* than in other sympatric krill species (Mauchline 1966; Sameoto 1980). Sameoto (1980) reported that *Thysanoessa* spp. in the Gulf of St. Lawrence fed primarily at night in the upper 75 m of the water column. Arctic and Antarctic euphausiids have been shown to be characterized by seasonally high lipid content. The Arctic

species *T. longicaudata* and *M. norvegica* feed on *Calanus* spp. as indicated by their high amounts of fatty acids.

Some marine mammals, such as whales, are known to feed almost exclusively on euphausiids, presumably on patches of high biomass. After the collapse of the Barents Sea Capelin stock in the early 1990s, Minke Whales in the northern part of the Barents Sea apparently switched from a Capelin-dominated diet to one almost completely comprised of krill, *Thysanoessa* spp. and *M. norvegica* (Haug *et al.* 2002a). Harp Seals are also key consumers of *Thysanoessa* spp. in certain areas (Nilssen *et al.* 1991). *Thysanoessa* spp. and *M. norvegica* were documented as winter (October to March) prey items for Thick-Billed Murres in western Greenland (Falk and Durinck 1993). Rowe *et al.* (2000) observed a decrease between the 1980s and 1990s in the proportion of *Thysanoessa* sp. in the stomachs of Thick-Billed Murres in Newfoundland. Euphausiids were the most abundant crustaceans in the murre diet except during October. Youngbluth *et al.* (1989) reported demersal fishes (cod, hake, pollock) and squid feeding on the epibenthic populations of euphausiids. Pacific Hake were identified as predators of *T. spinifera* off the southwest coast of Vancouver Island (Tanasichuk 2002). Dalpadado *et al.* (1996; 1998b; 2000) reported that herring fed on *M. norvegica* and *T. inermis* in February and March on the shelf and shelf edge off Norway. Diet investigations on young northeast Arctic Cod sampled in the Barents Sea between 1984 and 2002 indicated that 0 and 1 year old cod fed heavily on krill (*M. norvegica* and *Thysanoessa* spp.) (Dalpadado and Bogstad 2004). Capelin is another primary predator of *Thysanoessa* spp. in the Barents Sea (Dalpadado and Skjoldal 1996). Gislason and Astthorsson (2000; 2002) also studied the feeding habits of spring spawning herring off Norway and found that euphausiids, primarily *M. norvegica* and also *Thysanoessa* spp., were the most important prey during June.

Relation to Man

Ecologically, krill are an important trophic link between small phyto/zooplankton and most fish species and large predators in the top trophic level (Nicol 2003). The study of krill is interdisciplinary crossing boundaries using a combination of oceanography, biochemistry, physiology, evolution and ecology to understand their role in the ecosystem (Mangel and Nicol 2000). Fossi *et al.* (2002) proposed a suite of biomarkers in *M. norvegica* as a potential multi-disciplinary diagnostic tool for assessment of the health status of a whale sanctuary in the Mediterranean Sea.

A Nova Scotia commercial fishery for krill has been proposed during the late 1990s, targeting the aquaculture feed market (Harding 1996). DFO first issued zooplankton harvest permits on the east coast of Canada in 1991. Exploratory fisheries occurred in the Gulf of St. Lawrence during 1993 to 1995, but landings were low. While *M. norvegica* is usually the target species for commercial exploitation in eastern Canada, *Thysanoessa* spp. have been fished in the Laurentian Region (Sameoto and Cochrane 1996).

3.5.4 Sand Shrimp (*Crangon septemspinosa*)

General Distribution

In the northwest Atlantic Ocean, Sand Shrimp are found from the northern Gulf of St. Lawrence to eastern Florida (Squires 1990). It occurs from the lower intertidal zone to depths of 450 m

(Gosner 1979; Corey 1980), but primarily from 0 to 90 m (Squires 1990). Around Newfoundland, Squires (1990) indicated that Sand Shrimp are widely distributed inshore, while off Nova Scotia and the U.S. an offshore distribution is more evident.

Life Cycle

Spawning and Fertilization: After overwintering in the offshore region, adult Sand Shrimp migrate inshore to spawn (Viscido *et al.* 1997). In Port au Port, Newfoundland, 4 mm carapace length (CL) females produced two batches of eggs during the summer within an eelgrass (*Zostera* sp.) community. Between May and September, water temperatures at this eelgrass habitat ranged from 8 to 25 °C (Squires 1965). In Passamaquoddy Bay, New Brunswick, Corey (1987) reported that Sand Shrimp have two separate spawning periods; spring spawning from March to early June and summer spawning from mid-July to August. Spring spawning involved primarily larger older females (~10 to 11 mm CL), while the smaller, younger females (~ 8 mm CL) predominated the summer spawning. The spring and summer water temperature ranges were 5 to 6 °C and 12 to 14 °C, respectively. This Sand Shrimp species exhibits continuous spawning in the southern part of its range. The transition between continuous and discontinuous spawning appears to occur between latitudes 42 °N and 44 °N.

Fertilized Eggs and Larvae: Berried females in the Mystic River Estuary, Connecticut, did not concentrate along the shoreline until the end of April, reaching peak concentration by mid-May. The berried females collected in the spring carried, on average, 2,400 to 3,500 eggs per female. Abundance and clutch size decreased in the summer and slightly increased again in the fall, but not to spring levels. While the majority of females collected in the spring were along the shoreline, those collected in the fall were primarily found in deeper water. Females carry the fertilized eggs until hatching occurs (Modlin 1980).

The time lapse between the appearance of the first ovigerous females in shallow water (late March-early April) and the first occurrence of post-larvae (mid-July) was approximately 10 to 12 weeks. Water temperature increases during that period ranged from 6.5 to 10 °C. Embryonic development lasted 10 weeks at 6 to 10 °C and only 4 weeks at 14 °C. Therefore, the female spring spawners carried the fertilized eggs more than twice as long as females who spawned during the warmer summer months (Corey 1980). Timing of larval release in Sand Shrimp is geographically variable, but at the northern end of its distribution, hatching occurs sometime between June and September.

Temporal and spatial distribution of the planktonic larvae indicated that hatching was not continuous. There appeared to be two periods of hatching; mid-April to early May and early June. Areas of larvae collections ranged in salinity from 9 to 25 ppt, the greatest concentration occurring in surface waters having a salinity of 20 ppt. Peaks in juvenile abundance occurred in deepwater in June ($156/m^2$), mid-July ($120/m^2$) and mid-November ($142/m^2$) and along the shoreline in mid-July ($38/m^2$) and mid-August ($20/m^2$) (Modlin 1980). Wehrtmann (1991) found that the critical feeding periods for larval development were the first 24 hours after hatching, Stage III and metamorphosis to juvenile stage.

Plankton sampling in Chesapeake Bay resulted in over 94% of all Sand Shrimp larvae catches occurring in April compared to sampling in February, June and August (Wehrtmann 1994). Early stages (I and II) accounted for over 81% of collected larvae, with April and June collecting all developmental stages, including juveniles. Sand Shrimp larvae were collected during nighttime hours at three stations off the New Hampshire coast between January 1978 and December 1980 (Grabe 2003). Surface and bottom salinities ranged from 28.8 to 33.8 ppt and 30.5 to 33.8 ppt, respectively. Lowest salinities were observed during April to June, while the highest salinities occurred between November and January. Two of the sampling stations were over coarse sand substrates at depths ranging from 20 to 27 m. The other sampling station was over ledge and boulder substrate in water depths ranging from 13 to 22 m. Sand Shrimp larvae were very abundant between March and December, especially during the June to September period. Stage I zoeae of Sand Shrimp were particularly abundant during spring to fall of each year, typically peaking between mid-May and late June. Stage I densities were highest at water temperatures $\geq$ 10 °C. Post-larval concentrations peaked between July and September, with highest densities occurring at water temperatures $\geq$ 16 °C.

Newly hatched larvae occurred over a wide salinity range (22 to 33.6 ppt), while more advanced stages were found primarily at higher salinities (> 30 ppt). The highest larval abundances (> 50 larvae m^3) were found in water temperatures between 10 and 14 °C. The highest abundances of early stage larvae (I and II) were collected in areas with the highest chlorophyll concentrations. This may indicate that phytoplankton play some stimulus role for larval release and then subsequently become the food source for the larvae (Wehrtmann 1994).

Squires *et al.* (1997) conducted plankton surveys during May to September at depths of < 9 m, not more than 20 m offshore at St. Chad's, Newfoundland. Occurrences of Stage I zoea of the Sand Shrimp showed three peaks; the first in early June, the second in early July and a third in August, perhaps indicating three separate spawning/hatching periods. Zoeal stages later than Stage I occurred as early as June and megalopa appeared in early July. Two peaks of occurrence of each zoeal stage between II and IV indicated at least two broods during the summer. Large numbers of all stages were caught during surface tows in August, when water temperatures were as high as 16 °C.

Juveniles and Adults: Corey (1980) collected monthly samples of the Sand Shrimp at two shallow water sites in Passamaquoddy Bay, New Brunswick during the period of May 1972 to August 1974. The post-larval young (0.5 to 1.0 mm CL) appeared in the benthos from about mid-July to mid-October, during which time there was one summer peak and one fall peak. The summer recruits remained in the shallow water until late September-early October, while and the fall recruits remained in the shallow water over the winter. By July, some of the older preceding fall recruits had reached sexual maturity and a few of the larger females were ovigerous. From late July through August, most of the fall recruits had left the shallow water areas and had been replaced by the summer recruits. Ovigerous females first appeared in late March-early April with newly extruded eggs. The CLs of ovigerous females present during late March-August period ranged from 6 to 14 mm. By late August, hatching had occurred from the eggs of about one-third of the ovigerous females. Water temperatures during February-March and August ranged from 0 to 1.3 °C and 12.5 to 14.3 °C, respectively.

Modlin (1980) presented the results of Sand Shrimp sampling in the Mystic River Estuary, Connecticut. Body lengths of male and female Sand Shrimp can reach 47 mm and 70 mm, respectively (Price 1962). Adults were rarely encountered at salinities less than 20 ppt. Adults larger than 30 mm CL were transitory in that they entered the deep water of the study area in late March and within one month they were concentrated along the shoreline. Once the water temperature reached 20 °C in early summer, these larger adults disappeared from the shoreline and only returned in the fall once water temperatures were again less than 20 °C. Smaller adults (< 30 mm CL) were common within the study area for most of the year, being most abundant by mid-August. They remained along the shoreline until water temperatures fell below 10 °C in November. While the temperature remained above 10 °C, these smaller adult Sand Shrimp did not mix with the recently settled juveniles (96% were < 6 mm CL) in deeper water.

Raposa and Oviatt (2000) studied the associations between a nekton community (fishes and decapods) and temperate seagrass beds (*Zostera marina*) off Long Island, New York, between June and October. Water depths at all of the sandy bottom stations was approximately 1 m. Sand Shrimp accounted for 69% of the decapod abundance and were predominantly young-of-the-year and juveniles. The Sand Shrimp, similar to other decapods, were most abundant at stations outside the salt marsh in the cove (i.e., away from the shore). Only Sand Shrimp were consistently caught on unvegetated bottoms, although they were more abundant in the eelgrass beds.

Viscido *et al.* (1997) examined the seasonal and spatial patterns of an epibenthic decapod crustacean assemblage off New Jersey at monthly intervals over a one-year period. The study was conducted around a coarse sand ridge with water depths ranging from 8 to 16 m. The substrate inside the ridge was predominantly mud and clay/sand, while outside the ridge it consisted of coarse sand/shell and clay/sand areas. *Crangon septemspinosa* densities were much lower on top of the ridge than to either side of it. Peak Sand Shrimp densities occurred in May and October landward of the ridge and in October and January on the seaward side of the ridge. These shrimp were virtually absent from the catches during June to August, at which time temperature stratification was substantial. Surface and bottom temperatures ranged from 2 to 22 °C and 2 to 19 °C, respectively, while salinities ranged from 28 to 34 ppt. Possible reasons for avoidance of the ridge top include reduced protection from predation due to lessened burial ability in coarse substrate and decreased ability of this shrimp to chemically detect infaunal prey due to the higher hydrodynamic flow on the ridge. Rountree and Able (1992a) reported that *C. septemspinosa* was one of the five most important species found in a New Jersey polyhaline subtidal marsh creek estuary during spring, summer and fall. Water temperature ranges were 7 to 10 °C (spring), 10 to 25 °C (summer and fall), while the salinity ranged from 23 to 33 ppt.

During a study conducted in a subestuary of Chesapeake Bay between May and October, 1989 to 1992, Ruiz *et al.* (1993) found that *C. septemspinosa* were always most abundant at depths less than 70 cm, but also occurred out to depths of 4 m. The water temperature and salinity ranges were 2 to 30 °C and 3 to 17 ppt, respectively. Contrary to patterns observed with other invertebrates at the site, Sand Shrimp did not exhibit any size variation over the depth range. Ruiz *et al.* (1993) speculated that the lack of size variation was due to the animal's capability of burying itself in the fine substrate in order to avoid predation.

A study of microhabitat preference at a deep water site (55 m) on the outer northwest Atlantic continental shelf indicated that *C. septemspinosa* distribution was positively correlated with sandy areas (Malatesta *et al.* 1992). Lazzari (2002) quantified species richness and abundance of epibenthic fishes and decapod crustaceans occurring in nekton assemblages in eelgrass (*Zostera marina*) and unvegetated sandy habitats in two mid-coastal Maine estuaries between August and November. Surface water temperatures were consistently above 15 ºC between August and late September, after which they decreased to about 9 ºC by November. The salinity was generally > 27 ppt. Sand Shrimp dominated decapod catch-per unit-effort and density in both estuaries and habitats.

Sand Shrimp are known to prey actively on small crustaceans (Price 1962; Welsh 1970; Olmi and Lipcius 1991). Based on laboratory experimentation, Witting and Able (1995) suggested that predation by Sand Shrimp may be an important determining factor of habitat selection, size and mortality during settlement of Winter Flounder and other benthic fishes. This Sand Shrimp has been shown to be an important epibenthic predator on small (< 3 mm shell height) Atlantic Surfclams (Viscido 1994) and juvenile Winter Flounder (Witting and Able 1995; Stehlik and Meise 2000; Taylor 2003; Taylor and Collie 2003a; b) and other flatfish (Bertram and Leggett 1994). Small gastropods and bivalves have also been found in the guts of Sand Shrimp (Squires 1965).

The Sand Shrimp plays an important role in food energy transfer in tidal marsh-estuarine ecosystems. They form a very important part of the diets of many commercially and non-commercially important fish. In a New Jersey estuary, Sand Shrimp are prey for flounder during late spring/early summer (Manderson *et al.* 2000). Rountree and Able (1992b) found the same trophic relationship in a subtidal polyhaline marsh creek estuary in New Jersey. Rountree and Able (1996) reported predation upon Sand Shrimp by juvenile Smooth Dogfish in the same polyhaline marsh creek estuary, particularly in June and July. Sand Shrimp were shown to be prey of Striped Bass (*Morone saxatilis*) in salt-marsh habitats in New Jersey (Tupper and Able 2000) and of bluefish (*Pomatomus saltatrix*) young-of-the-year in Long Island waters (Juanes *et al.* 2001). *C. septemspinosa* are often associated with Hermit Crab (*Pagurus acadianus*) and Rock Crab (*Cancer irroratus*) (Squires 1990). Double-crested cormorants in Maine are known to forage on this Sand Shrimp (Blackwell *et al.* 1995).

This shrimp species has been identified as a key animal species of the biota assemblage associated with the "seagrass bed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. These areas typically have sand to fine gravel substrates that are stable and not subject to excessive erosion, are often but not necessarily estuarine and ice-covered in winter and are sheltered (low exposure to wave energy) (Hooper 1997). In Newfoundland, examples of this habitat type are St. Paul's Bay, Piccadilly Harbour in Port au Port Bay, Mortier Bay, North Harbour in St. Mary's Bay and Bellevue in Trinity Bay (Hooper 1997).

Relation to Man

An experimental fishery for this Sand Shrimp was conducted in Chaleur Bay, southern Gulf of St. Lawrence in 1997. Both day and night trawls were conducted during five surveys, which occurred from August to November. Very few Sand Shrimp were caught within the depth range

of 20 to 82 m, supporting the belief that they are most abundant in shallow water estuaries and bays and that the only viable way to commercially fish for Sand Shrimp would be to use shrimp traps set in shallow water (Hanson and Lanteigne 1999). In addition to its potential direct significance to the commercial fishery, *C. septemspinosa* also plays an important role as a food source for numerous commercial species.

3.5.5 Snow Crab (*Chionoecetes opilio*)

Distribution

Snow Crab occupy a broad depth range in the northwest Atlantic Ocean from Greenland to the Gulf of Maine (DFO 1989b; 2003c; 2004b). The species typically occurs on soft bottoms at depths of 60 to 400 m where water temperatures remain primarily between –1 and 6 °C (DFO 2007d). Temperatures > 7 °C are known to be detrimental to Snow Crab (DFO 2008c).

In Newfoundland and Labrador, there are no known barriers to larval drift or settlement, or any other evidence to indicate distinct stocks. Dawe *et al.* (2003) described the fall spatial distributions of male and female Snow Crab throughout NAFO Divisions 2GHJK3LMNO during the 1995 to 2002 period, based on fall bottom trawl surveys. In 2002, the fall distribution of males was generally similar to the distributions observed between 1995 and 2001. Males of all sizes were absent from the deepest sets (> 500 m) along the slope of Division 3K, but they did occur at greater depth along the slopes of Divisions 2J and 3LN. Males were essentially absent in the shallow southern Grand Bank in Divisions 3LN. The largest males were found along the 3LN slope region, while large males were typically absent on the innermost (< 300 m) sets in 2J3K. Both female and male Snow Crab were virtually absent over a broad area of the shallow southern Grand Bank (< 100 m). Mature female Snow Crab distribution in 2002 continued to be similar to that of comparably sized males.

Life Cycle

Spawning and Fertilization: Prior to copulation, the male retains the female in a precopulatory embrace and drives away intruding males for the period leading up to the female's molt (Elner and Beninger 1995). Once the female has molted with assistance from the male, copulation occurs. Bright orange fertilized eggs are extruded onto the female's pleopods within 24 hours of copulation (Elner and Beninger 1995). The female can also extrude subsequent clutches of eggs fertilized by spermatophores stored in her ventral spermathecae. Snow Crab can extrude up to approximately 128,000 eggs. Taylor (1996) looked at the egg numbers of 350 Snow Crab collected from Newfoundland waters. The fecundities of these females ranged from 8,500 to over 103,000, averaging just below 45,000 per female. Individual fecundity was positively correlated with size. The female Snow Crab carry the fertilized eggs until larval hatching.

Large numbers of sexually paired Snow Crab have been observed in relatively shallow water (10 to 40 m) during late April-early May at Bonne Bay, Newfoundland (Taylor *et al.* 1985; Hooper 1986; Ennis *et al.* 1990). The pairs were found in algal covered boulder slopes less than 1 km away from areas of depth > 100 m. Level sand or mud substrates supported lower densities of paired Snow Crab, but were the main sites where feeding was observed.

Fertilized Eggs and Larvae: There are uncertainties regarding the duration of the reproductive cycle in female Snow Crab (Elner and Beninger 1995). Originally, the females were assumed to have a 12-month cycle between egg extrusion and larval hatching, but subsequent research indicated that the time between extrusion and hatching can be as long as 27 months. Embryonic development proceeds faster in warmer water, regardless of depth (Moriyasu and Lanteigne 1998). Larval hatching appears to be triggered by the sedimentation peak of phytoplankton particles (phyto-detritus) originating from the surface spring bloom (Starr *et al.* 1994), introducing another variable into the estimation of development time.

The lag time between peak phytoplankton bloom and hatching in the April-June period (Comeau *et al.* 1999) ensures the full development of microzooplankton on which the larvae feed. The larvae, initially known as zoea I stage, spend 12 to 20 weeks as plankton and molt through two more stages (zoea II and megalopae) before settling to the bottom (Roff *et al.* 1984a). The examination of environmental stock relationships for some marine invertebrate species in Newfoundland Shelf waters (Colbourne *et al.* 2002) indicated that cold conditions early in the life cycle (i.e., pelagic larval stage or settling megalopal stage) of Snow Crab are favourable for early survival. The lethal temperature for megalopae is around 18 °C (DFO 2007c). Larvae are vulnerable to predation by larger planktivores.

Neuston net sampling on the Scotian Shelf in the 1970s captured Snow Crab larvae up to 230 km from shore at temperatures ranging from 5.6 to 18.6 °C and salinities of 30 to 32.4 ppt (Roff *et al.* 1984b). Ocean currents can transport larvae considerable distances from their hatching location before fall settlement occurs. Nearshore (< 20 m from shore) plankton sampling was conducted at St. Chad's, Bonavista Bay, Newfoundland from May to September at different depths (< 9 m) and distances from shore (Ennis 1983a; Squires *et al.* 1997). Stage I Snow Crab larvae were taken primarily at the surface during onshore wind conditions. No adult female Snow Crab were found, suggesting that the larvae moved inshore with onshore winds. Occurrences of the Snow Crab Stage I zoea showed two peaks; one in mid-June and another in early to mid-July. Sainte-Marie *et al.* (1995) reported that male Snow Crab in a Gulf of St. Lawrence population recruited to the legal carapace width (CW) of 95 mm approximately 8 to 9 years after settlement.

Juveniles and Adults: Commercial size Snow Crab (males > 94 mm CW) in Newfoundland and Labrador are most common on a mud or mud/sand bottom, while smaller crabs are common on harder substrates as well. Robichaud *et al.* (1989) found that Snow Crab density in the southeastern Gulf of St. Lawrence was related more to substrate than to depth. They found that juveniles (< 50 mm CW) were densest on mud, although all sizes were found on the three substrates (mud, sand and gravel) sampled. Juvenile and mature female crabs were patchily distributed within each substrate type. Brêthes *et al.* (1987) found a wide distribution of early benthic Snow Crab (< 30 mm CW) over areas off the north shore of the Gulf of St. Lawrence at water temperatures less than 3 °C, sediments containing more than 40% mud and depths $\geq$ 60 m. Results of laboratory experiments indicated that early benthic stages of Snow Crab displayed sharp size-age-dependent distributions and habitat preferences (Dionne *et al.* 2003). When placed in a temperature gradient of 0 to 2.5 °C, Instar III crabs selected water temperatures of 0 to 1.5 °C and concentrated in mud rather than sand or gravel, Instar IV crabs did not exhibit any temperature or substrate preferences and Instar V crabs selected temperatures of 1 to 2.5 °C, but

no specific substrate. In a temperature gradient of 1.5 to 4.5 °C, Instar V crabs did not exhibit any temperature preference, but did select mud more often than other substrates. In the warmest thermal gradient (3 to 5.5 °C), a preference for temperatures of 3 to 4.5 °C was observed, but there was no specific substrate preference. Dionne *et al.* (2003) also conducted observations in the field. They noted that Instars I to IV were scarce in the core of the cold intermediate layer with temperatures < 0 °C, but were present immediately above and below this layer where temperatures were higher. Older juveniles (Instars VI to VIII) were concentrated at depths < 27 m above the cold intermediate layer, reflecting the higher temperature shift between Instars III and V in the laboratory experiments. In summary, water temperature and substrate appear to play central roles in the distribution of juvenile Snow Crab. Effects of temperature differ throughout the life cycle. Cold conditions in early life favour survival, while later in life they promote early terminal molt, thereby reducing the proportion that will recruit to the fishery (DFO 2008d). Higher temperatures may cause females to change their reproductive cycle from two years to one (DFO 2007c).

The Snow Crab was one of the nine most dominant species, in terms of biomass, collected by epibenthic sled on a sandy bottom on the Grand Banks of Newfoundland at depths of 120 to 146 m (Prena *et al.* 1999). Snow Crab catches by otter trawling were also common during this experiment.

In Conception Bay, Newfoundland baited traps were set at various depths (20 to 210 m depth range) during a continuous 13-month period (Miller and O'Keefe 1981). Snow Crab depth distribution was generally deeper than 90 m and individual size increased with depth and changed seasonally. At 90 m, Snow Crab were largest between September and February. Bottom temperatures at depths ≥ 90 m deeper ranged from –1.1 to 1.1 °C during the 13-month period.

Depth distributions and seasonal movements of juvenile and adult Snow Crab in the northern Gulf of St. Lawrence were studied by Lovrich *et al.* (1995). Water depths in the study area ranged from 4 to 140 m. Immature crabs of 3 to 10 mm CW were found predominantly in 50 to 80 m of water where they were cryptic and sedentary. Most immature crabs ranging from 14 to 35 mm CW, as well as adolescent males, migrated in winter to subtidal grounds in order to molt. Adult males less than 70 mm CW also moved to shallower grounds during October to December, where some mated with primiparous females during January to April. Adult males exceeding 90 mm CW were primarily found at depths > 80 m during most of the year, except from March to May. During this period larger adult males moved upslope to shallower water, probably to mate with multiparous females. Adult females were more gregarious and sedentary than the adult males. The temperature and salinity ranges over the 4 to 140 m depth range of the study area were –1 to 5 °C and 30 to 33 ppt, respectively.

Comeau *et al.* (1998) studied a relatively unexploited stock in Bonne Bay, Newfoundland. In the study, relative abundance of early benthic to commercial size individuals suggested that small immature crabs migrate from shallow rocky areas to deep muddy bottom areas. The patchy spatial distribution observed for the Snow Crab in Bonne Bay appeared to be determined more by substrate and intra-specific factors than by depth. Seasonal movements to shallow waters by larger crabs were related to density and temperature dependent factors associated with the

reproductive and growth cycle. Comeau *et al.* (1998) also reported life expectancies of female and male Snow Crab in Bonne Bay, Newfoundland of 13 and 19 years, respectively.

Hooper (1986) observed the feeding behaviour of sexually paired Snow Crab in shallow water at Bonne Bay, Newfoundland during April and May. The most favoured natural prey types of the Snow Crab were polychaetes, ophiuroids and bivalves, although the most frequently eaten food was fish used as lobster bait. In stomach contents of Snow Crab caught at 210 m in Conception Bay, Newfoundland between June and November, polychaetes, clams and sea stars were the dominant prey items (Miller and O'Keefe 1981).

Predators of juvenile and adult Snow Crab include various groundfish, other Snow Crab and seals. Predation on recently settled Snow Crab by older juvenile cohorts could be an important regulatory process for Snow Crab (Sainte-Marie and Lafrance 2002). Robichaud *et al.* (1986; 1991) found that Atlantic Cod off Cape Breton were feeding mostly on large, softshelled male Snow Crab during April and May. Snow Crab were still found in cod stomachs collected during July and September. More Snow Crab were taken by the cod over sand and mud bottoms than over rocky and gravel substrates. Robichaud *et al.* (1986; 1991) also detected substantial predation on Snow Crab by thorny skate.

Relation to Man

The Newfoundland and Labrador Snow Crab commercial fishery landings in NAFO Divisions 2J3KLNOP4R have increased steadily from 1989 to peak at 69,000 mt in 1999 at a value of over $236 million (DFO 2007e), largely due to expansion of the fishery to offshore areas (DFO 2007f). There are indications that exploitable biomass of this species has been declining since 1998. Landings decreased by 20% to 55,400 t in 2000 and remained fairly stable until they decreased to just over 47,000 mt in 2006 at a value of over $1 million (DFO 2007e; 2007f). Longer term recruitment potential is uncertain, but the persistence of a warm oceanographic regime implies poor prospects relative to the strong recruitment of the late 1990's (DFO 2007f).

3.5.6 Rock Crab (*Cancer irroratus*)

General Distribution

Rock Crab are found in the northwest Atlantic Ocean from southern Labrador to Miami, Florida at depths ranging from the low water mark to 575 m (Williams 1984). Distribution records for the Atlantic coast of Canada indicate inshore occurrences only (Squires 1990). This crab species is most common in shallow water (< 20 m), especially in bays on open sand or sand/mud bottoms (DFO 1989b; 2000c). Hudon and Lamarche (1989) found that in the southern Gulf of St. Lawrence, Rock Crab were most abundant on rocky substrates colonized with macroalgae, but they also inhabited bare rocky substrates, eelgrass beds and bare sandy substrates. This crab is common along the coastlines of Newfoundland and Nova Scotia, in the southern Gulf of St. Lawrence (DFO 2002) and the Bay of Fundy. In the northern part of its range, the Rock Crab is generally found in 5 to 20 m of water, while to the south it occurs primarily in deeper waters (DFO 1996h). Data obtained from groundfish trawl and clam dredge surveys conducted from 1978 to 1987 on the continental shelf from Nova Scotia to Cape Hatteras, revealed that Rock Crab distribution ranged from depths of 6 to 456 m (Stehlik *et al.* 1991).

Life Cycle

Spawning and Fertilization: The Rock Crab typically attains sexual maturity within 3 to 6 years of age (DFO 1996h). Mating takes place when the female is in softshell condition, typically in April and May (Tremblay and Reeves 2000). Egg incubation usually occurs during mid- to late fall (late October) and continues until the following spring/summer (Bigford 1979).

Fertilized Eggs and Larvae: The number of eggs carried by the female Rock Crab is dependent on the size of the female. For example, a 60 mm carapace width (CW) female can carry approximately 125,000 fertilized eggs, while a 90 mm CW female may carry as many as 500,000 (Tremblay and Reeves 2000; DFO 2007g). Rock Crab carry the fertilized eggs for approximately 4 months at which time larval hatching occurs (as early as mid-June) (DFO 2008e).

Larval hatching generally occurs during the warmer late spring/summer months. The free-swimming larvae immediately join the near surface plankton and remain there for up to 3 months. Hudon and Fradette (1993) described the wind induced advection of larval decapods, including Rock Crab, into a bay of the Magdalen Islands in the southern Gulf of St. Lawrence. They discussed the chance factor of sporadic wind events coinciding with times of peak larval abundance. Rock Crab larvae are initially positively phototactic, but change abruptly to positive geotaxis in preparation for settlement. Field studies have suggested that the maximum depth of decapod larval vertical migration is determined by the position of the thermocline (Harding *et al.* 1987). Settlement resulting in highest survival most often occurs inshore on gravel/cobble substrate with kelp cover.

The Rock Crab larvae molt through six stages (5 zoeas and 1 megalopa) before settlement to the seabed (Roff *et al.* 1984a). Rock Crab larvae are omnivorous planktivores. They are prey to larger zooplankton and planktivorous fish.

Plankton sampling was conducted in Bonavista Bay, Newfoundland from May to September at different depths and distances from shore (Ennis 1983a; Squires *et al.* 1997). With onshore wind conditions, Rock Crab larvae were generally most abundant at the surface, but also occurred in substantial numbers at 3 m and were less frequent at 6 and 9 m. From mid-June to early August, water temperatures ranged from 7.6 to 15.2 °C, but little vertical stratification was evident during any given sample time. The highest abundances of Rock Crab larvae occurred in samples collected during the first two weeks of July (water temperature range of 7.8 to 10.0 °C). Within the surface layer, the concentration of larvae varied with distance from shore (< 2 to 20 m), but not in any consistent pattern. Stages 1, 3 and 4 zoeas and megalopae were all present in the sampled larvae. Clancy and Cobb (1997) studied the association between wind/tidal advection and abundance of Rock Crab megalopae off Rhode Island during an eight-year period. The considerable inter-annual variation in average daily abundance of the neustonic larvae was evident from their work. Neuston net sampling on the Scotian Shelf in the 1970s captured Rock Crab larvae from surface waters of temperatures ranging from 2 to 22 °C and salinities ranging from 28 to over 35 ppt (Roff *et al.* 1984b).

Rock Crab larvae were far more abundant in the upper 40 m of the water column at the head than at the mouth of Conception Bay, Newfoundland (Pepin and Shears 1997). Mean catches of Rock Crab larvae (per thousand m^3) at the head of the bay during late July and early August ranged from 5,420 to 25,000, while mean catches at the mouth of the bay during the same period ranged from 66 to 3,650. Rock Crab larvae have been found in densities as high as 50,000/1,000 m^3 of water, which is comparable to Lyre Crab, but substantially greater than American Lobster (Hudon and Fradette 1993).

Juveniles and Adults: Palma *et al.* (1998; 1999) found that Rock Crab in the Gulf of Maine showed considerably less discrimination among habitat types and environmental conditions during settlement than did lobsters. By virtue of their high fecundity, Rock Crab have high rates of settlement and suffer high levels of post-settlement mortality relative to lobsters. Newly settled Rock Crab were found in a wider variety of substrates and depth range and in considerably lower salinities in estuarine habitat (Clancy and Cobb 1995).

After settlement, the Rock Crab grows through a multiple molt juvenile stage, reaching sexual maturity within 3 to 6 years. In the Northumberland Strait, females attain 50% sexual maturity at a carapace width of 55 to 60 mm, while males are mature at 70 mm CW. Size at maturity is smaller at more southern latitudes (Bigford 1979). Juveniles (15 mm) are found mainly at shallow depths on bottoms that offer shelter from predators and water turbulence (DFO 2007g). As the crab grows through juvenile and adult stages, their sheltering needs change and preference shifts to coarser substrates (i.e., large cobble, boulder) mixed with patches of finer substrate suitable for burrowing. Gibeault (1995) concluded that the more complex habitats in the Gulf of Maine supported a greater diversity of Rock Crab sizes than more uniform habitats. He found that Rock Crab exhibits substantial variation in habitat used during its life cycle. Himmelman (1991) also reported that Rock Crab in the northern Gulf of St. Lawrence show broad habitat preferences, occurring on both rocky and soft bottoms. Given the large degree of overlap of American Lobster and Rock Crab distributions, many habitat requirements of lobster can be applied to juvenile and adult Rock Crab.

The Rock Crab is one of the major predators in northern subtidal communities, whereas fish and decapod crustaceans are the predominant predators in more southern communities (Himmelman 1991). Juvenile and adult Rock Crab diet includes juvenile Sea Scallops (Barbeau *et al.* 1996a; Lafrance *et al.* 2003; Weissberger and Grassle 2003), juvenile Iceland Scallops (Arsenault and Himmelman 1996a), mussels (Ojeda and Dearborn 1991), snails, Green Sea Urchins (Himmelman and Steele 1971), brittle stars, amphipods, Sand Shrimp and polychaetes (Squires 1965; Stehlik 1993). Moody and Steneck (1993) discussed the apparent functional dichotomy between large decapods, such as *H. americanus* and smaller ones like *Cancer irroratus*. Rock Crab are capable of a greater diversity of predatory shell opening tactics than the American Lobster. Large Rock Crab are known to take small lobster (Hudon and Lamarche 1989), a species with which they often share habitat. Morissette and Himmelman (2000a) described this crab's as a kleptoparasite with the sea star *Leptasterias polaris*, especially when the sea star was feeding on large clams. Wong and Barbeau (2003) investigated the effect of substrate on predation of juvenile Sea Scallops by Rock Crab at two prey sizes and two prey densities under laboratory conditions. They found that substrate type (glass bottom, sand, granule, pebble) did

not have any significant effect on the predation rate of Rock Crab on scallops of either size. However, Rock Crab did tend to predate more on smaller scallops.

Groundfish and lobster (Bigford 1979; Carter and Steele 1982; Tremblay *et al.* 2001; Sainte-Marie and Chabot 2002; DFO 2008e) are the primary predators of Rock Crab. Gendron *et al.* (2001) discussed the importance of Rock Crab as prey for the growth, condition and ovary development of adult American Lobster. If stranded in the intertidal zone, Rock Crab may be vulnerable to predation by sea birds (Dumas and Witman 1993). Rock Crab were identified as the principal diet item of Smooth Dogfish caught off Chesapeake Bay (Gelsleichter *et al.* 1999).

Relation to Man

This crab species generally occurs as a by catch in the lobster fishery and is subsequently used as bait. Commercial fishing of the Rock Crab in Atlantic Canada has been limited over the years. During the early 1980s, annual landings from the Northumberland Strait in the southern Gulf of St. Lawrence reached 500 mt at a value of over $110,000 (DFO 1989b). Its small size, low meat yield and high processing costs have limited its commercial appeal (Elner 1985). An exploratory inshore fishery for Rock Crab was conducted in the Gulf of Maine between 1995 and 2000 (Robichaud *et al.* 2000). In Newfoundland and Labrador, Rock Crab landings were only 93 mt in 2006, with an estimated value of $71,675 (DFO 2007e).

Despite its limited commercial value, the Rock Crab is very important ecologically as it is a principal prey species of lobster, which is a major commercial species in Atlantic Canada. Rock Crab are also considered a good bioindicator animal for monitoring the quality of the marine environment (Chou *et al.* 2002b).

3.5.7 Lyre (Toad/Spider) Crab (*Hyas araneus, Hyas coarctatus*)

Distribution

Lyre Crab are found on both sides of the North Atlantic Ocean in depths ranging from the shallow subtidal to more than 700 m (Squires 1965; Williams 1984). Lyre Crab are very common near most of the coastline of Newfoundland and Labrador and also occur on the continental slopes from Labrador to the Grand Banks. These crabs occur predominantly at intermediate depths, essentially overlapping the conventional inshore Rock Crab/lobster and offshore Snow Crab areas (DFO 1996i). *Hyas araneus* tends to be found in slightly shallower water than *Hyas coarctatus* (Miller and O'Keefe 1981).

H. coarctatus is represented by 2 subspecies: *H.c. alutaceus* and *H.c. coarctatus*. Although there is individual variation in size between the two subspecies, nonetheless they can be separated on the basis of size, morphology and distribution (Pohle 1991). The two subspecies overlap in their distribution in the North Atlantic, however *H.c. alutaceus* is restricted to the Northwest Atlantic (Rathbun 1925). In the western Atlantic Ocean, *H. araneus* occurs from Greenland to Rhode Island and *H. coarctatus* is more widely distributed from Hudson Bay and Greenland to Cape Hatteras (Squires 1990). Tavares and De Melo (2004) reported the discovery of *H. araneus* in Antarctica. This is the first known benthic invasive species in the Southern Ocean.

Life Cycle

Spawning and Fertilization: Petersen (1995) collected female *H. araneus* with newly extruded eggs during the spring in the North Sea, indicating springtime spawning in that area. Squires (1990) took mature female *H. coarctatus*, most carrying eggs, from Hudson Bay, Labrador and Newfoundland during May to November. Most of the females also had large ova in their ovaries indicating that spawning would occur after the eggs hatched each year.

Lyre Crab are unusual among most crustaceans in that they become sexually mature only after they undergo the final ecdysis. Therefore, mature individuals cannot grow any more (Hartnoll *et al.* 1993). *H.c. coarctus* as small as 20 mm carapace length (CL) have been determined to be sexually mature. Bryant and Hartnoll (1995) found that most *H. coarctatus* in the Irish Sea attained terminal molt during May to July, followed immediately by mating and egg laying. Hatching of the larvae occurred the following March or April.

Fertilized Eggs and Larvae: Squires (1990) indicated that berried females carry the eggs for approximately 10 months. Mathieson and Berry (1997) found egg carrying *H. araneus* from February to November in a Scottish estuary. Brood weights of *H. coarctatus* in the Irish Sea were approximately 10% of the female body weight (Bryant and Hartnoll 1995).

Petersen (1995) concluded that *H. araneus* embryonic development might possibly extend to two years under certain conditions. He found that incubating fertilized eggs at 12 °C during the last three months of development resulted in higher mortality and reduced hatching success than incubating at 6 °C. Larvae typically hatch during the warmer summer months and remain in the upper water column plankton for one to several months as they molt through three stages; 2 zoeas and 1 megalopa (Roff *et al.* 1984a). Roff *et al.* (1984b) reported the size range of the three larval stages caught off Nova Scotia as 1.07 to 3.20 mm. Lyre Crab larvae are planktivorous and, in turn, are subject to predation by other zooplankton and planktivorous fish.

Davidson and Chin (1991) captured and held berried *H. araneus* in the laboratory at 3 to 5 °C. Hatching occurred in late March and larvae were then introduced to 10 to 12 °C water. Despite substantial water temperature and salinity variability, the larvae displayed resilience and low mortality and commenced metamorphosis approximately 100 days after hatching. Other laboratory testing of *H. coarctatus* larvae indicated that larval mortality was highest at temperature extremes (18 °C and 6 °C) than at intermediate temperatures (9 to 15 °C) (Anger 1984).

Field studies have suggested that the downward limit of decapod larval vertical migration is determined by the position of the thermocline (Harding *et al.* 1987). Plankton sampling was conducted in Bonavista Bay, Newfoundland from May to September at different depths and distances from shore (Ennis 1983a; Squires *et al.* 1997). Zoeal stages 1 and 2 Lyre Crab larvae were taken in large numbers (> 400) during one sampling time in July, when the temperature throughout the water column was 8.3 °C. They were much more abundant at the surface than at depths from 3 to 9 m and were more abundant with onshore winds than with offshore winds. Eighty percent of the Lyre Crab larvae were collected about 4 m from shore. During plankton surveys from 1985 to 1987 and 1991 to 1992 in the northern Gulf of St. Lawrence, *Hyas* larvae

were among the earliest ones caught in large numbers each year, usually in May (Ouellet *et al.* 1994).

Densities as high as 50,000 larvae per 1,000 m^3 seawater have been sampled (Hudon and Fradette 1993). As with most zooplankton, dispersion of Lyre Crab larvae is dependent primarily on oceanic currents/water movements considering the limited swimming ability of the larvae. Hudon and Fradette (1993) described the wind-induced advection of larval decapods, including Lyre Crab, into a bay of the Magdalen Islands in the southern Gulf of St. Lawrence. They discuss the chance factor of sporadic wind events coinciding with times of peak larval abundance. Roff *et al.* (1984a) reported the capture of *Hyas* larvae up to 310 km from the Nova Scotian shore at temperatures of 0 to 20 °C and salinities of 29 to 33 ppt.

Juveniles and Adults:
Anger (1984) found that the *H. coarctatus* larval phase lasted approximately 80 days. He predicted that settling and metamorphosis occurs mainly in June. Lyre Crab appear to prefer gravel, sand or mud substrates. Gilbert *et al.* (1984) reported the presence of Lyre Crab in the subtidal zone (15 to 45 m) below an intertidal flat area near Nain, Labrador. This area had a cobble/pebble substrate and strong currents. Barrie (1979) reported Lyre Crab at three Labrador locations with sandy substrates over depths of 1 to 36 m. Himmelman (1991) reported that Lyre Crab in the northern Gulf of St. Lawrence show broad habitat preferences, occurring on both rocky and soft bottoms. Other decapod species often taken with *H. araneus* and *H. coarctatus* include *Pandalus* sp. and *Pagurus pubescens* (Squires 1965). *Chionoecetes opilio* is also a common species caught with *H. coarctatus*.

In Conception Bay, Newfoundland, baited traps were set at various depths (20 to 210 m depth range) during a continuous 13-month period (Miller and O'Keefe 1981). Lyre Crab depth distribution was generally in the 20 to 55 m depth range and individual size was relatively constant with depth and time of year. Bottom temperatures in this distribution area ranged from –1.1 to 13.0 °C. Mathieson and Berry (1997) discussed *H. araneus* occurring year round in a Scottish estuary, where salinities ranged from 22 to 31 ppt in the summer, but dropped as low as 12 ppt in the winter.

H. araneus was not taken in the Arctic where *H. coarctatus* was common (Squires 1990). It did occur inshore in Labrador at water temperatures of –1.3 to 6.3 °C and offshore (35 to 730 m) at temperatures of 0.8 to 3.6 °C. It was also present in the Gulf of St. Lawrence deep water community of *P. borealis,* where positive temperatures prevail throughout the year, indicating *H. araneus* has a preference for warmer waters than *H. coarctatus*. Specimens of *H. coarctatus* were reared under laboratory conditions at ambient temperature conditions until they had undergone at least two molts (Hartnoll and Bryant 2001). Inter-molt period and percentage increment either decreased with increasing temperature or showed no response.

The Lyre Crab is one of the major predators in the more northern subtidal communities, whereas fish and decapod crustaceans are the predominant predators in more southern communities (Himmelman 1991). Their diet includes amphipods, euphausiids, copepods, polychaetes, hydroids, bivalves, ophiuroids, gastropods, chitons, sea urchins, small crab and scavenged fish (Squires 1965). Arsenault and Himmelman (1996b) concluded that at their study site in the

northern Gulf of St. Lawrence, *H. araneus* was the major predator of juvenile Sea Scallops. Morissette and Himmelman (2000a) described Lyre Crab as kleptoparasites of *Leptasterias polaris,* especially when the sea star was feeding on large clams. *H. coarctatus* larvae appear able to develop normally on a diet of particular diatoms, whereas *H. araneus* larvae seem to require an animal diet (e.g., *Artemia*) (Harms and Seeger 1989).

Predators include groundfish species and various decapod crustaceans (DFO 1996i). Robichaud *et al.* (1986; 1991) reported a higher occurrence of Lyre Crab in the stomachs of cod caught over rocky, gravel bottom than those taken over a mud/sand bottom. They also observed predation of Lyre Crab by Thorny Skate. Guillemette *et al.* (1992) reported Common Eiders feeding on Lyre Crab in *Agarum* beds in the Gulf of St. Lawrence. Studies on the feeding habits of Bearded Seals in Norway identified *H. araneus* as a common crustacean prey item (Hjelset *et al.* 1999).

Relation to Man

Lyre Crab has recently been the target of exploratory commercial fisheries in Newfoundland and Nova Scotia. This crab species has been targeted in Newfoundland waters since 1994. Prior to 2000, most of the fishing activity occurred in the area between White Bay and Bonavista Bay, but it has expanded since then in order to test other areas and a variety of depths. Overall, the development of this fishery in Newfoundland has been slow (FDP 2002). In 2006, Lyre Crab landings were approximately 613 mt in Newfoundland and Labrador, valued at close to a $500,000 (DFO 2007e). *H. araneus* has been considered as a bioindicator species in polar ecosystems. Camus *et al.* (2002) established biomarkers that could be used with this Spider Crab species.

3.5.8 Hermit Crab (*Pagurus* spp.)

General Distributions

Three boreal species of Hermit Crab (*P. acadianus, P. arcuatus and P. pubescens*) occur in Canadian waters of the northwest Atlantic Ocean. They are generally found in the shallow subtidal zone, *P. pubescens* tending to occur deeper than the other two (Gosner 1979). Distribution records around Newfoundland and Labrador indicate that *P. acadianus* only occurs in inshore areas (Squires 1990). The area of occurrence of *P. acadianus* extends from the Strait of Belle Isle, Notre Dame Bay in Newfoundland and the Gulf of St. Lawrence to Chesapeake Bay. Documented depths of occurrence range from 0 to 485 m. In Newfoundland, *P. arcuatus* and *P. pubescens* occur both inshore and offshore. *P. arcuatus* occurs from Greenland to the Virginia Capes (Squires 1990) over a depth range of 0 to 270 m. The distribution of *P. pubescens* extends up the Labrador Shelf as far north as Hudson Bay, Ungava Bay and Foxe Basin, west of Greenland. It occurs as far south as Cape Hatteras (Squires 1990).

Life Cycles

Spawning and Fertilization: Seventy-five percent of the female *P. pubescens* examined in Foxe Basin were potentially ovigerous in autumn indicating annual spawning in that area (Squires 1990). Wada *et al.* (2000) described the reproductive traits of four species of *Pagurus*, demonstrating the reproductive diversity within four sympatric, congener species.

Fertilized Eggs and Larvae: Squires (1990) noted that ovigerous *P. acadianus* were taken from Cape Cod Bay during January and March (Williams 1984). The fertilized eggs are carried on the female crab's pleopods until hatching occurs. The planktonic larval stage at hatching is the zoea. Roberts (1973) reported that development time from larval hatch (4 stages to megalopa stage) was approximately 40 days.

Squires (1996) described the larvae of *P. arcuatus* collected from the plankton at St. Chad's, Newfoundland in 1971. He also indicated the presence of larvae of the other two Hermit Crab species in the plankton samples. Squires *et al.* (1997) found that occurrences of Stage I zoea of *P. acadianus* showed two major peaks during the summer at St. Chad's, perhaps indicating two hatching periods in the warm, shallow waters. The sampling was conducted within 20 m of shore at depths not exceeding 9 m. Three times as many *P. arcuatus* larvae than *P. acadianus* larvae were collected by Squires *et al.* (1997). *P. arcuatus* larvae showed three peaks (early June, early July and mid-August). Captures of late zoeal stages of both species occurred in surface tows in late July over the deeper water areas. Megalopae did not appear until mid-August. The water temperature measured at the St. Chad's study site ranged from 2 °C in early June to almost 12 °C in late August at a depth of 9 m (Squires *et al.* 2000). Squires *et al.* (2001) indicated that both *P. acadianus* and *P. arcuatus* at St. Chad's hatch in early spring, extrude eggs in late autumn and carry the eggs through the winter.

The distributions of various meroplankton, including those of various *Pagurus* species, were investigated off southern Washington in May 1999 (Roegner *et al.* 2003). Both estuarine and open coastal ocean areas were surveyed. *Pagurus* spp. larvae were rare in the riverine plume water, but were found in higher concentrations in recently upwelled areas nearshore. Hermit Crab megalopae tend to be more abundant at night. Miller and Shanks (2004) also found that *Pagurus* spp. megalopae were most abundant in the open coastal ocean area than in the estuary off the coast of Oregon. In Japan, Oba and Goshima (2004) found differences in the spatial patterns of larval settlement between two Hermit Crab species (*P. middendorfii* and *P. nigrofascia*). Settlement periods of these two Hermit Crab species fully overlapped so their larvae were most probably affected by similar transport factors such as current and tidal movement.

Juveniles and Adults: On Georges Bank, Hermit Crab were found to be more abundant at shallow sites (42 to 47 m) than at deeper ones (80 to 90 m) in both April and November (Collie *et al.* 1997). Larger Hermit Crab were found at the disturbed deep water sites compared to the undisturbed deep sites, possibly due to migration into the disturbed areas to feed on animals damaged as a result of bottom trawling.

Barrie (1979) reported *P. arcuatus* in 3 to 18 m of water at different locations in Labrador over predominately sandy substrates. He also found *P. pubescens* at Nain, Labrador on sandy substrates over a depth range of 22 to 56 m. All three *Pagurus* species appear to have a preference of occupying empty *Buccinum* sp. shells (Williams 1984). Grant (1963) discovered this same shell preference by *P. acadianus* in Maine, with next preferred shells being *Thais* sp. and *Littorina* sp.

Van Winkle *et al.* (2000) studied the effects of *Pagurus longicarpus* on the interactions of epibiont species that comprise the communities encrusting the crab shells. They specifically looked at two hydroid species. Results suggested that Hermit Crab invariably affect colony polyp number, colony morphology and the outcome of inter-specific competition. It is likely that the mechanisms underlying these effects include hydrodynamics and mechanical disturbance. Reiss *et al.* (2003) discussed the ecological importance of shells inhabited by the Hermit Crab (*P. bernhardus)* as a hard substrate in soft bottom habitats in the North Sea. In the Hermit Crab sampled during the summer at five stations in the North Sea, 51 epizoic species were found. As many as 427 individuals and 15 species were found on an individual Hermit Crab. The most abundant epizoans included polychaetes, cnidarians, crustaceans and balanids. McDermott (2001) described the biotic symbiotic association of the gastropod shell-*P. longicarpus* complex in New Jersey. The association included species from eight phyla. A worldwide review of the symbiotic associates of Hermit Crab was prepared by Williams and McDermott (2004).

Hooper (1997) identified Hermit Crab as key organisms of the biotic assemblage associated with the "scallop bed" habitat type he characterized as a type of marine coastal habitat in Newfoundland and Labrador. Typical physical characteristics described for this habitat type include sand/gravel/shell substrates and wide ranges of water temperature and exposure to wave energy (Hooper 1997). Himmelman (1991) reported the occurrence of Hermit Crab in two types of subtidal region in the northern Gulf of St. Lawrence; 1) moderately exposed, medium-sloped bottom at 5 to 10 m and 2) gently sloping sediment bottoms in areas of strong tidal current at 10 to 15 m.

Squires (1965) identified stomach contents of all three Hermit Crab species. Fish offal, crustacean fragments and mussel shells were found in *P. acadianus*, phytobenthos, foraminiferans, small bivalve shell, crustacean fragments, small gastropods, hydroids and ophiuroids were found in *P. arcuatus*; and phytobenthos, foraminiferans, amphipods, ostracods, bivalve fragments, ophiurans, polychaetes and hydroids were found in *P. pubescens*. *P. longicarpus* is considered to be a predator of newly settled surfclams, *S. solidissima* (Weissberger and Grassle 2003). Whitman *et al.* (2001) discussed the suspension feeding behaviour of *P. longicarpus*, a Hermit Crab species specialized for this mode of feeding. While several studies support the view that Hermit Crab are primarily benthic detritovores, some species appear capable of some form of filter-feeding, especially from the surface boundary layer that contains bacteria, diatoms, protozoans and other organic material (Scully 1978).

Relation to Man

P. acadianus (and most likely the other two Hermit Crab species) has been identified as an important prey of commercially significant groundfish species (skates, cod and hake). *Pagurus* spp. have also been investigated as potential biological control species of fouling in suspended scallop (*Pecten maximus*) cultivation in the Irish Sea off the Isle of Man (Ross *et al.* 2004).

3.6 ECHINODERMATA

3.6.1 Green Sea Urchin (*Strongylocentrotus droebachiensis*)

General Distribution

The Green Sea Urchin has a circumpolar distribution and is present on both coasts of North America. On the east coast of North America from Baffin Island south to New Jersey, it is a common inshore species (maximum depth of 40 to 60 m) wherever salinity is greater than 15 ppt. Green Sea Urchins are generally most abundant immediately below the subtidal algal fringe at a depth range of 5 to 10 m (Hawkins 2000).

Until recently, it was believed that there was a single species of sea urchin in Newfoundland and Labrador waters. However, it is now known that there are two morphologically distinct species. The Green Sea Urchin is a coastal shallow water species, while *S. pallidus* is typically found at greater depths (> 60 m) and is widespread on the Grand Banks (Gagnon and Gilkinson 1994). Taxonomic and ecological studies of *S. pallidus* in the region can be found in Gagnon and Gilkinson (1994) and Gilkinson *et al.* (1988).

In Newfoundland, this species is commonly found in shallow subtidal areas over stable rocky substrates (cobble, rubble boulder) with at least medium energy exposure (DFO 1996j). The Green Sea Urchin has been identified as being responsible for the presence of "sea urchin barrens" or areas where macroalgae have been almost completely eliminated due to excessive herbivory from high densities of sea urchins (Lawrence 1975). The geology of this habitat type generally includes bedrock and/or boulders. Other physical characteristics typically include full salinity, some current effect, moderate to full exposure to wave energy and the ability to withstand major ice scour (Hooper 1997).

Life Cycle

Gametogenesis: Himmelman (1977) described the reproductive cycle of Green Sea Urchins (> 30 g) at Portugal Cove, Newfoundland for a one to two-year period. He found that the gonadal index peaked in late winter and early spring, just prior to spawning and gonadal growth was dependent on food availability. Meidel and Schleibling (1998) also monitored the reproductive cycle of the Green Sea Urchin, but they compared populations in different habitats (kelp beds, barren grounds and grazing fronts) and under varying exposure conditions (wave exposed and sheltered) along the coast of Nova Scotia. They found that the reproductive cycle was synchronous across all conditions and between males and females. Spawning generally occurred between March and April of each year, although small proportions of the populations spawned during the fall of one year. Gonadal indices were highest in urchins living in kelp beds and grazing fronts, particularly under wave exposed conditions. Rogers-Bennett *et al.* (1995) suggested that the supply of drift algae might be greater at wave exposed sites due to plant dislodgement and transport by the increased wave action. On the other hand, Ebert (1968) and Gonor (1973) found lower sea urchin gonadal indices in exposed areas, possibly due to the high energy expenditure towards spine repair. These gonadal index differences were probably mostly due to differences in diet. The high density of sea urchins in grazing fronts combined with their higher fecundities suggested that they contributed most to the larval pool on a per unit area basis.

Walker and Lesser (1998) concluded that photoperiod is correlated with the initiation of gametogenesis in the Green Sea Urchin. Hooper and Cuthbert (1993) reported high roe yields in September during a survey of sea urchins in southern Labrador.

The effects of temperature and food ration on gonad growth and oogenesis of *Strongylocentrotus droebachiensis* were investigated through laboratory experimentation in Maine (Garrido and Barber 2001). Sea urchins collected in December and June were kept for three months under treatments of varying temperature and ration levels. Primary oocytes of the winter collected sea urchins were significantly larger in individuals held at 3 °C than at 12 °C, regardless of level of food ration. The primary oocytes of the summer collected sea urchins were significantly larger in individuals receiving higher food rations, regardless of temperature. The results indicated that conditions of high food availability in summer and low temperatures in winter favour reproductive output in Green Sea Urchin populations.

Spawning and Fertilization: The Green Sea Urchin generally spawns during the spring to early summer period once conditions such as water temperature and food availability (phytoplankton) are favourable for fertilization and subsequent embryonic and larval development. Keats *et al.* (1987) reported some summer and fall spawning in Newfoundland waters. Spawning is a rapid event in this species. The variable time period between gonadal maturity and spawning may indicate that the spawning is triggered externally. Himmelman (1977) found substantial variability in water temperature at time of spawning (from < 3.0 to 8.0° C), leading him to conclude that temperature alone does not stimulate spawning in the Green Sea Urchin. There appears to be a stronger synchrony between spawning and the spring phytoplankton bloom (Starr *et al.* 1990). Female urchins may release between 100,000 to 2 million eggs into the water column where external fertilization occurs. Since urchin sperm has a life span of only 20 to 30 minutes, successful fertilization in the water column depends on the synchronization of gamete release by individuals in the same aggregation. Hooper and Cuthbert (1993) discuss the concept of "mass spawning" wherein the majority of individuals within a population spawn at the same time. Through both laboratory and field work, Pennington (1985) showed the importance of male-female proximity and current strength to successful fertilization.

Meidel and Schleibling (2001) modeled temporal and spatial patterns in egg spawning in the shallow subtidal zone along the Atlantic coast of Nova Scotia. They predicted that the number of eggs spawned per m^2 is one order of magnitude higher in sea urchin grazing fronts than in transitional and post-transitional barrens and 4 to 6 times higher in barrens than in established kelp beds. They estimated fertilization rates in grazing fronts at 62%, transitional and post-transitional barrens (36 and 43%, respectively) and kelp beds 15%.

Yund and Meidel (2003) studied fertilization processes in sea urchins induced to spawn in a benthic boundary layer in a flow-through flume with the male urchin located approximately 0.5 m upstream of the female. They found that fertilization levels declined only slightly with increasing flow velocity, suggesting that fertilization in echinoderms with viscous, long-lived gametes could be much less sperm-limited than thought. Laboratory experimentation has shown that Green Sea Urchin eggs have high viability for two to three days after release (Meidel and Yund 2001).

Fertilized Eggs and Larvae: Fertilized eggs initially sink to the bottom, but rise to the surface waters within 1 to 3 days for larval hatching. Eggs undergo normal development within a –1 to 11° C temperature range (Himmelman 1977). The free-swimming larvae hatch and can remain planktonic for 2 to 5 months, using cilia to feed. The upper water temperature limit for larval development is around 10 °C (Stephens 1972). Larval sea urchins require uncontaminated seawater of suitable temperature (< 10 °C) and salinity (> 20 ppt) (Hawkins 2000) and a sufficient supply of phytoplankton as a food source. Roller and Stickle (1985) studied the effects of salinity on embryonic and larval development of the Green Sea Urchin. Fertilized eggs were placed into seawater of varying salinities (20 to 30 ppt) and observed for 32 days. Although development was slower at 25 ppt and lower than at 27.5 and 30 ppt, the eggs and larvae survived all treatments.

Bertram and Strathmann (1998) concluded that although maternal habitat had a large effect on fecundity and egg size, growth of the larvae was minimally affected by differences in the maternal habitat. In general, maternal nutrition was better in shallow areas compared to deeper areas and in barrens as compared to kelp beds (Bertram and Strathmann 1998). Meidel *et al.* (1999) reported that when food was abundant, larvae of adults from nutritionally rich habitats tended to metamorphose sooner than those from nutritionally poor habitats. A study by Burdett-Coutts and Metaxas (2004) suggested that larvae of *S. droebachiensis* are able to actively aggregate and maintain a vertical position in response to a quality food patch. They also suggested that this response is based on a chemosensory rather then a mechanosensory mechanism.

Sea urchin larvae are vulnerable to predation by certain zooplankton and surface feeding fish species. Eventually they settle to the ocean bottom and metamorphose to the initial post-larval urchin stage (juvenile) within hours. Balch and Scheibling (2000) investigated temporal and spatial variability in settlement and recruitment of Green Sea Urchins in kelp beds and barrens in Nova Scotia over a three-year period. Settlement pulses occurred between July and September. Although they found that Green Sea Urchin settlement was greater in the barrens than the kelp beds, the difference was not statistically significant. This could have been due to the kelp beds filtering out the settlers before they reached the collectors on the bottom. Balch and Scheibling (2000) also found that recruitment of Green Sea Urchins in barrens was about twice that in the kelp beds, suggesting higher juvenile mortality in the kelp beds. Their study demonstrated the importance of settlement and post-settlement processes in determining the population structure, distribution and abundance of a mobile benthic marine invertebrate with dispersing larvae.

Settlement timing and differential settlement of Green Sea Urchin larvae was studied in the southern Gulf of Maine during the summer (Lambert and Harris 2000). Settlement densities were highest in June and early July, peaking in mid-June. Settlement was negligible from mid-July to the end of August. No substrate preference was exhibited during peak settlement, but during the remainder of the settlement period there appeared to be a preference for substrate with coralline algae. Newly settled urchins on the coralline algae tended to be larger. Sustained onshore winds occurred during peak settlement.

Juveniles and Adults: Survival of post-larval sea urchins is highest on kelp covered rock substrate in relatively shallow water. Temperature, intolerance to low salinity levels, lack of

food and shelter availability are some of the factors responsible for the wide variability in juvenile growth and survival. Low salinity levels are particularly harmful to smaller juveniles of 5 to 10 mm test diameter (Himmelman *et al.* 1984). After settlement, prey preference broadens considerably to include dead organic material. Common food sources include fleshy macrophytes (*Laminaria* spp. and *Alaria* spp.), detritus and various marine organisms. Age and size at sexual maturity ranges from 4 to 10 years and 18 to 25 mm diameters, respectively (DFO 1996j). It is noteworthy, however, that difficulty in determining sea urchin age as a function of size has been reported (Russell *et al.* 1998; Russell and Meredith 2000).

Adult sea urchins are able to live in a diverse range of habitats due to their generalist diet, but tend to be most fit in areas of stable substrates (bedrock/boulder) with substantial kelp growth (Moore *et al.* 1986). Adult urchins are quite sensitive to reduced salinity levels (20 ppt) (Himmelman *et al.* 1984). Adults prefer water temperatures ranging from 0 to 10 °C and although they may tolerate temperatures as high as 20 °C (Hawkins 2000), they are more prone to pathogenic induced mortality at temperatures $\geq$ 12 °C (Brady and Scheibling 2005). Work by Drouin *et al.* (1985) in the northern Gulf of St. Lawrence suggested that salinity fluctuations have an important impact on echinoderm populations probably due to the high permeability of their outer surfaces. Sea urchin abundance was lower at depths < 4 m in areas with substantial salinity flux (6 to 30 ppt) compared to areas where salinity was more stable (24 to 30 ppt). The sea urchins present in shallow water at the polyhaline site tended to be large. Other work has indicated that sea urchin tolerance to low salinity decreases with decreasing body size (Himmelman *et al.* 1984). Green Sea Urchins prefer areas with at least moderate energy exposure. Kraft and Gordon (2001) concluded that a fast current environment might be beneficial to sea urchin growth. Siddon and Witman (2003) examined the importance of hydrodynamic forces in causing patterns of subtidal zonation by looking at both wave exposed and sheltered sites in the Gulf of Maine. At the exposed site, *S. droebachiensis* were restricted to depths > 3 m, while their prey (mussels and kelp) dominated the shallower region (1 to 3 m). At the sheltered site, sea urchins foraged up to mean low water. Their study highlighted the importance of chronic, low level forces in the structuring of marine benthic communities. Adams (2001) examined the responses of Green Sea Urchins to ultraviolet radiation (UVR) under laboratory conditions and discovered that sea urchins seek shelters and cover in response to UVR, especially the UVB wavelengths.

Green Sea Urchins along with Horse Mussels were consistently deemed the most important assemblage components, in terms of biomass and density, during a study of the macroinvertebrate fauna inhabiting a rocky subtidal habitat in Maine (Ojeda and Dearborn 1989). Sea urchin density at this study site decreased with depth (from 5 to 18 m). The spatial distributions of the sea urchins and Horse Mussels strongly influenced the distribution and abundance patterns of other macroinvertebrates. Himmelman *et al.* (1983) demonstrated the structuring role of the Green Sea Urchin in a rocky subtidal zone located in the St. Lawrence Estuary. The temporal variation in community interfaces, specifically the kelp bed boundary dynamics adjacent to persistent sea urchin barrens, was studied by Gagnon *et al.* (2004) in the northern Gulf of St. Lawrence. They proposed that perturbations by abiotic factors (e.g., ice scouring and water motion) trigger important, but localized changes in urchin densities that, in turn, largely determine the limits of kelp bed distribution in this region of the Atlantic where urchin barrens are persistent. Study of size specific movement of Green Sea Urchins in the

northern Gulf of St. Lawrence indicated that urchins < 15 mm diameter exhibited a relatively sedentary and cryptic lifestyle compared to those > 15 mm diameter (Dumont *et al.* 2004). Larger urchins tended to show increased movement, probably related to the search for food. Increased wave action reduces displacement and contact rate of large (20 to 60 mm diameter) Green Sea Urchins towards algal prey (Gagnon *et al.* 2003a; 2006). Tegner and Dayton (2000) discussed the potential ecosystem effects of fishing on kelp community structure worldwide, focusing on fishing for sea urchins, their predators and their competitors.

Waddell and Perry (2007) surveyed Green Sea Urchin populations in Queen Charlotte Strait, British Columbia. They found the highest density of Green Sea Urchins was observed on creviced bedrock in the 1.2 to 0.0 m above chart datum (CD) range. The mean total densities generally decreased continuously with each increasing depth interval. The lowest total density occurred at the greatest depth range (12.5 to 13.4m) below CD.

In eastern Canada, destructive grazing of kelp by the Green Sea Urchin is a cyclical phenomenon (Scheibling *et al.* 1999; Gagnon *et al.* 2004). The rate of destructive grazing varies with wave intensity and nature of the kelp species (Gagnon *et al.* 2005; Lauzon-Guay and Scheibling 2007), resulting in less productive, coralline algal-dominated assemblages. Considering the large numbers of fish and invertebrates that utilize kelp beds as habitat, large scale shifts in community state occur when the urchins overgraze (Sivertsen 1997; Scheibling *et al.* 1999). Witman (1985) discussed how *S. droebachiensis* was the most significant agent of biological disturbance in a rocky subtidal community in New England over a five-year study period. This echinoderm caused a 79% reduction in the mean population density of invertebrates outside of the Horse Mussel beds which provide some refuge from grazing disturbance. Bulleri *et al.* (2002) discussed the interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. They suggested that the occurrence of areas dominated by encrusting corallines on shallow subtidal reefs in the Mediterranean Sea is not simply the result of grazing by sea urchins and that the role played by coralline algae in maintaining alternative habitats should be taken into account.

Hooper and Cuthbert (1993) reported the results of the first scientific investigation of sea urchin stocks in Labrador. Sea urchin abundances in Labrador were quite comparable to those found in Newfoundland, averaging about 50 individuals per m^2. The upper depth limit of Labrador sea urchins appeared to be deeper than those in Newfoundland, likely due to increased ice scour effect and lower salinities. Hooper and Cuthbert (1993) found that Labrador sea urchin populations included much older animals and fewer young animals than those around Newfoundland. These findings implied that sea urchins might have a lower natural mortality rate than those in Newfoundland and that recruitment in Labrador may be more episodic than in Newfoundland. The possible episodic nature of recruitment could make the Labrador sea urchin populations more vulnerable to population structure change due to fishing or natural perturbation. There was no evidence of sea urchin "mass spawning" during the Labrador study.

Russell *et al.* (1998) examined growth and mortality rates of mature Green Sea Urchins in Maine through a tagging study. Over 500 individuals from tide pools were tagged during 1994 and of the 458 urchins caught in 1995, 262 of them were tagged. Their findings concluded that the urchins were slow growing and long-lived, the age of the largest urchins being estimated at over

50 years. They found the maximum growth rate occurring in sea urchins with test diameters of 18 to 25 mm (3 to 12 years of age).

Despite a preference for macroalgae, Green Sea Urchins scavenges dead animals and drifting algae and even prey on other animals. In barren areas, sea urchins have been known to graze on diatoms attached to rocks and ingest sand to remove diatoms, radiolarians and other protozoa. Various studies have been conducted on the diet of the Green Sea Urchins (Himmelman 1984; Cuthbert *et al.* 1995; Cuthbert *et al.* 1996; Hooper *et al.* 1996; Lemire and Himmelman 1996; Minor and Scheibling 1997; Vadas *et al.* 2000). Himmelman and Steele (1971) conducted qualitative analysis of gut contents of Newfoundland sea urchins collected monthly between February and November. They found that perennial phaeophytes, mostly fucoids and *Alaria esculenta*, were predominant in the diet. Ephemeral algal species, coralline algae and animals (Blue Mussels, barnacles and periwinkles) were consumed in smaller quantities when available.

Primary predators of sea urchins around the Newfoundland coast include lobsters, crabs, sea stars, flatfish, wolffish (Liao and Lucas 2000), sculpins, Ocean Pout and sea birds (Himmelman and Steele 1971; Keats *et al.* 1986b; Keats 1991). *S. droebachiensis* have been shown to exhibit immediate behavioural responses to waterborne chemosensory cues from wolffish and crabs (Hagen *et al.* 2002). Sea birds also predate on sea urchins if they are accessible in the intertidal and high subtidal zones. Guillemette *et al.* (1992) documented the predation of Common Eiders (*Somateria mollissima*) on Green Sea Urchins over barrens and *Agarum* spp. beds in the Gulf of St. Lawrence. Although a pathogenic amoeba (*Paramoeba invadens*) has caused widespread mass mortalities of Green Sea Urchin in Nova Scotia over the last decades. This phenomenon has not been reported in northern regions of Atlantic Canada, including Newfoundland and Labrador (Scheibling 1984; Scheibling and Hennigar 1997; Gagnon *et al.* 2004)

Relation to Man

During the early to mid 1990's, various reports examining the potential of a commercial sea urchin fishery in Newfoundland and Labrador were published (Gillingham and Penny 1993; Dooley 1994; Eastman 1995). The conclusions were positive towards some level of a commercial sea urchin fishery. In Newfoundland, the sea urchin harvest in shallow subtidal areas is typically conducted by SCUBA diving. The timing of the harvest is critical since the targeted roe must be at a certain stage of development. In Newfoundland, the harvest usually occurs in late winter or early spring, prior to peak spawning time. Commercial harvesting of this species in Newfoundland has been conducted primarily in Trinity Bay and Conception Bay, with lesser efforts occurring in Placentia Bay and Fortune Bay. During 1998 and 1999, 850 to 927 mt were harvested annually in Newfoundland at a value of $1.16 to $1.32 million (DFO 2001b). In 2006, landings were only 235 mt with a value of $312,856 (DFO 2007e).

The effect of individual size and diet on gonad yield and quality in Green Sea Urchin was investigated by Pearce *et al.* (2004) under laboratory conditions using sea urchins collected from the Bay of Fundy. They found that after six weeks, the percent gonad yield in urchins fed a prepared feed diet was greater than those fed *Laminaria* spp. alone. They also indicated that percent gonad yield was greatest in urchins with a body diameter within the 40 to 50 mm range, followed closely by those 30 to 40 mm and 50 to 60 mm. In Newfoundland, Liyanapathirana (2001) investigated the quality of Green Sea Urchin roe in relation to season and dietary factors.

She reported that the effects of variations of feed supply and seasonal components on gonad quality were very evident.

A study of the impacts of scallop dragging initiated in New Brunswick in the early 1990s indicated that there was a significant decrease in sea urchin densities and an increase in the number of broken urchin tests after harvesting was conducted with commercial scallop drags (Robinson *et al.* 2001). Although the observable short term impacts from a single dragging event were gone after three months, the long-term effects remain unknown.

Antibacterial activity in different body parts of the Green Sea Urchin has been investigated in an effort to discover new sources of novel antibiotics (Haug *et al.* 2002b). While there was some haemolytic activity found in the sea urchin tissue, the level was lower than in two other echinoderms involved in the study; sea cucumber and Common Sea Star.

3.6.2 Orange-Footed Sea Cucumber (*Cucumaria frondosa*)

Distribution

The sea cucumber is found in the North Atlantic Ocean, its distribution ranging from the coast of northern Europe and Scandinavia to the Faroe Islands and southern Iceland, the coast of Greenland and southwest along the New England coast. It is one of the most abundant and widely distributed echinoderm species along the east coast of Canada. This species occurs from the Arctic to Cape Cod, from the lower intertidal zone and cold tide pools to deeper than 300 m in the subtidal zone (Gosner 1979). The sea cucumber is abundant at depths of less than 30 m on hard, rocky bottoms where it can constitute up to 70% of the epifaunal biomass. Densities are highest where water currents ensure a steady food supply for this suspension feeding species. Coady (1973) found abundant quantities of this sea cucumber throughout Newfoundland and at locations in Labrador, typically at depths < 30 m.

Life Cycle

Gametogenesis and spawning: Sexual maturity is generally attained by this species within 2.5 to 3 years. There is evidence for chemical mediation in the initiation of gametogenesis and inter-individual fine tuning among populations of *Cucumaria frondosa* (Hamel and Mercier 1996a). Hamel and Mercier (1996b) reported the occurrence of sea cucumber spawning in the lower St. Lawrence Estuary during mid-June. Males released the sperm first, followed by release of eggs by the females. Medeiros-Bergen and Miles (1997) reported sea cucumbers spawning in the spring in the Gulf of Maine. Spawning by these echinoderms in shallow water of the Avalon Peninsula, Newfoundland occurred between February and May (Coady 1973). Coady (1973) found that the timing of sea cucumber spawning in Newfoundland appeared to be closely associated with the spring phytoplankton bloom.

While previous studies on the reproductive cycle of echinoderms did not clearly demonstrate a single spawning event for *C. frondosa*, Singh *et al.* (2001) used more quantitative methods and were able to indicate a single sea cucumber spawning event in the spring.

Fertilization and Larval Development: Fertilized eggs and embryos are buoyant. Falk-Petersen (1982) determined that *C. frondosa* had larvae that underwent pelagic lecithotrophic development. According to Hamel and Mercier (1996b), embryonic development was fastest at 12 °C, pH of 8 and a salinity of 26 ppt under laboratory conditions. Furthermore, the free-swimming larvae (known as pentactulae) hatched approximately 9 days after fertilization and remained pelagic for 6 to 7 weeks (Hamel and Mercier 1996b). Medeiros-Bergen *et al.* (1995) found that sea cucumber larvae were in the water during April to June in the Gulf of Maine, the two largest pulses occurring at 20 m during June. Larvae of *C. frondosa* dominated the samples at almost every sampling station. In June, they recruited heavily to rock/gravel substrates (Medeiros-Bergen and Miles 1997), particularly in areas containing mussel beds. Mussel beds may enhance survival of newly settled sea cucumbers by providing a refuge from predation.

Juveniles and Adults: After 4 to 5 months at an approximate length of 3 mm, young sea cucumbers move to sheltered, illuminated areas of rocky substrate (Hamel and Mercier 1996b). Miles (1995) reported that higher abundances of juvenile sea cucumbers (1 to 4 mm length) were found in coralline algae compared to kelp holdfasts, mussel beds and vertical rock faces along the coast of New Hampshire. Once they grow to about 35 mm length, the sea cucumbers migrate from protected to exposed areas. Hamel and Mercier (1996b) showed a size-dependent migration from photic to aphotic depths (> 40 m) when the animals reached sexual maturity. Potential predators of new recruits are large nereid worms (Medeiros-Bergen and Miles 1997).

Adults normally occur in small dense beds on rock or gravel substrates. Legault and Himmelman (1993) found that sea cucumbers in the northern Gulf of St. Lawrence were most common on bedrock to cobble substrates at depths ranging from 4 to 15 m. Himmelman (1991) reported the occurrence of *C. frondosa* in three of the types of subtidal regions in the northern Gulf of St. Lawrence; 1) moderately exposed, medium sloped bottoms at 4 to 8 m, 2) exposed, gently sloped bedrock platforms at 10 to 15 m and 3) gently sloped sediment bottoms in areas of strong tidal currents at 10 to 15 m. They are filter feeding planktivores, using the ten tentacles surrounding the mouth (DFO 1997d). Orange-Footed Sea Cucumbers are passive suspension feeders in that they depend entirely on ambient water movements to drive water through their filtering tentacles (LaBarbera 1984). Hamel and Mercier (1998) found that *C. frondosa* in the St. Lawrence estuary fed mainly during spring and summer on phytoplankton, small crustaceans and a variety of eggs and larvae. They observed that feeding rates were highest during ebb and rising tides, but concluded that food availability rather than physical parameters such as temperature or current best explains the cyclic feeding behaviour of the Orange-Footed Sea Cucumbers at seasonal and tidal scales. Laboratory controlled feeding experiments by Singh *et al.* (1998) implied that in the natural environment, sea cucumbers maximize ingestion when the chloropigment concentration in the seston increases.

Field observations in the Bay of Fundy over three years revealed a seasonal feeding rhythm for *C. frondosa* at depths ranging from 5 to 16 m (Singh *et al.* 1999). They extended their tentacles and commenced feeding in March-April and ceased feeding in September-October, possibly in response to change in day length.

Field observations and intestinal contents analysis (Hamel and Mercier 1998) demonstrated that sea cucumbers from the St. Lawrence Estuary fed mainly during spring and summer. Diet was

comprised primarily of various species of phytoplankton, with occasional occurrences of small crustaceans and a variety of eggs and larvae. Limited feeding in fall and winter was primarily on detritus. Sea stars, lobsters and Snow Crab have been reported to prey on sea cucumbers (Scarrat 1980; Elner and Campbell 1987; Himmelman 1991; Wieczorek and Hooper 1995).

Relation to Man

Gudimova (1998) indicated that *C. frondosa* from the Barents Sea is being utilized in the pharmological industry. Also, antibacterial activity in different body parts of the sea cucumber has been investigated in an effort to discover new sources of novel antibiotics (Haug *et al.* 2002b). *C. frondosa* has quickly become one of the world's most important commercial sea cucumbers (Therkildsen and Petersen 2006). However, fisheries for this species are still in an early stage and predictions about their future sustainability are difficult to make (Therkildsen and Petersen 2006).

3.6.3 Brittle Stars (*Ophiopholis aculeata*; *Amphipholis squamata*; *Ophiura* spp.)

General Distributions

In the northwest Atlantic Ocean, the Daisy Brittle Star (*Ophiopholis aculeata*) occurs from the Arctic south to Cape Cod, often under rocks in tide pools located in the lower intertidal zone. This Arctic-boreal species has been found as deep as 1,500 m (Gosner 1979). *A. squamatus* is believed to be the only viviparous echinoderm with a worldwide distribution. Its distribution in the northwest Atlantic Ocean extends from the Arctic south to Long Island Sound. It is also often found among stones and debris in large tide pools of the intertidal zone, but it also occurs subtidally on gravel substrates from shallow water depths to > 300 m (Gosner 1979). Other documented habitats include coralline algae and other phytal communities, stands of mussels, bryozoans and burrowed into loose substrates. Its vertical distribution has been documented as deep as 1,330 m (Jones and Smaldon 1989). In the northwest Atlantic Ocean, *Ophiura robusta* occurs from the Arctic to Cape Cod, while *Ophiura sarsi* occurs only as far south as Maine. *O. robusta* is primarily subtidal, but it does occur in the lower intertidal zone from the Bay of Fundy northward. *O. sarsi,* an Arctic-boreal species, generally inhabits the subtidal zone at depths of 9 m or more (Gosner 1979).

General Life Cycle of Ophiuroids

Ophiuroids undergo asexual reproduction in addition to sexual reproduction. Hendler (1991) discussed the environmental factors believed to influence spawning in brittle stars. These factors include water temperature, food availability, currents, light and lunar cycles.

The majority of ophiuroids are dioecious. Some species exhibit external fertilization, while others brood. In non-brooding oviparous ophiuroids, early development is similar to that of asteroids. The common ophiuroid larva is known as an ophiopluteus. Hart (1991) described the feeding methods employed by various echinoderm larvae, including the ophiopluteus of *O. aculeata*. Metamorphosis takes place while this larva is still free-swimming. The Tiny Brittle Star sinks to the bottom, often heterogeneous in nature (e.g., rock, kelp) and begins its adult existence. Time from fertilization to settlement ranges from 14 to 40 days. To reach the same stage in the brooding species, *A. squamatus* takes 3 to 7 months (Barnes 1980).

Balch *et al.* (1999) found that most of the settling by *O. aculeate* and *Ophiura* spp. in St. Margaret's Bay, Nova Scotia occurred during a two-week period in late July to early August, when water temperature ranged between 12 and 14 °C and salinity was between 30 and 31 ppt. They were most struck by the finding that settlement of a species with such long-lived planktonic larvae (up to 7 months) can occur over such a short period, in association with low amplitude fluctuations in the physical environment (temperature and salinity). Although settling occurred in both a kelp bed area and a barrens area, both within a depth range of 6 to 10 m, the ophiuroids showed a trend towards greater settlement in the barrens (Balch and Scheibling 2000).

Ophiopholis aculeata: Falk-Petersen (1982) determined that *O. aculeata* in the North Sea bred mainly during late spring/summer and that subsequent larvae underwent pelagic planktotrophic development. Larvae of the brittle star *O. aculeata* on the North Pacific coast of the U.S. undergo asexual reproduction of the primary larva to produce a secondary larval clone (Balser 1998), potentially increasing the geographic range and the number of juveniles of a given parentage in future generations without additional reproductive input from the adult.

Work by Drouin *et al.* (1985) in the northern Gulf of St. Lawrence suggested that salinity fluctuations have an important impact on echinoderm populations probably due to the high permeability of their outer surfaces. *O. aculeata* abundance was lower in water shallower than 4 m in areas with substantial salinity flux (6 to 30 ppt) compared to the other areas where salinity was more stable (24 to 30 ppt). Himmelman (1991) reported the occurrence of *O. aculeata* in two of the types of subtidal regions in the northern Gulf of St. Lawrence; 1) moderately exposed, medium-sloped bottoms at 3 to 8 m and 2) exposed, gently sloped bedrock platforms at 0 to 10 m.

Carter and Steele (1982) reported that the Daisy Brittle Star was one of the more dominant prey items found in the guts of immature lobster collected from Placentia Bay, Newfoundland during June to November. This brittle star species occurred in 34% of the lobsters, dominated the stomach contents of 15% of the lobsters and accounted for 33% by weight of the stomach contents of the lobster in which it was found. The percentage frequency of its occurrence was highest during late August to mid-September (50%) and ranged from 26 to 33% the rest of the time. Carter and Steele (1982) estimated its percentage contribution to the total volume of the immature lobster population diet to be slightly over 11%, ranking third behind Rock Crab (14.8%) and mussels (11.6%). This brittle star was the primary prey item of American Plaice throughout the year (Falk-Petersen 1982). The Common Sea Star (*Asterias rubens*) has also been identified as a predator of *O. aculeata* (Gaymer *et al.* 2001a; 2001b), especially in subtidal areas below the mussel zone.

Amphipholis squamata: *A. squamatus* is a small, synchronous hermaphroditic brittle star. It is the only brittle star species within the distribution range that incubates its young. It can simultaneously brood several embryos at different stages of development in each of its ten genital bursae (Walker and Fineblit 1982). In Scotland, *Amphipholis squamata* has continuous brooding and pulsed breeding and recruitment, with highest numbers of brooded embryos and newly released juveniles occurring in the summer months. The majority of emergent juveniles had a disc diameter ranging from 0.8 to 1.2 mm (Jones and Smaldon 1989). They also found brittle stars with full stomachs throughout the year, although feeding was more prevalent during

spring and summer. A wide range of plant and animal food items were identified in its diet including strands of green algae, arm fragments of *Amphipholis* and crustacean appendages.

Hooper (1997) identified this genus of brittle star as a key taxon in the biota assemblage associated with the "coralline algal bed" habitat type characterized as a type of a marine coastal habitat in Newfoundland and Labrador. Spaces in the corallines provide unlimited shelters for the brittle stars. Coralline algal bed habitats are characterized by bedrock and boulder substrates with patches of rhodoliths and sediments. Other physical characteristics include full salinity, strong currents and moderate to high exposure to wave energy. Hooper (1997) also observed that brittle stars (unspecified species) are key animals in "lobster ground" habitat.

Ophiura spp.: *O. sarsi* was the second most dominant species, in terms of biomass, collected by epibenthic sled on a sandy bottom on the Grand Banks of Newfoundland at depths of 120 to 146 m (Prena *et al.* 1999). Himmelman (1991) reported the occurrence of *O. sarsi* in two of the types of subtidal regions identified in the northern Gulf of St. Lawrence; 1) moderately exposed, medium-sloped bottoms at 3 to 8 m and 2) exposed, gently sloped bedrock platforms at 0 to 10 m. Piepenburg and Schmid (1996) described epibenthic brittle star assemblages at 80 to 360 m depth on the Barents Sea Shelf, including *O. sarsi*. Seasonal and annual variability of an epifaunal assemblage in the German Bight area of the North Sea was described by Hinz *et al.* (2004) over a four-year period. The study area had a depth range of 38 to 42 m and quite variable levels of mud and total organic carbon. Despite the environmental variability, *Ophiura* spp. was common throughout the study area.

Packer *et al.* (1994) examined the population structure of *O. sarsi* in an area in the Gulf of Maine at 150 m depth. They observed that major spawning occurred in January despite evidence of continuous, albeit seasonally variable, reproduction. Falk-Petersen (1982) determined that *O. sarsi* in the North Sea bred mainly during late spring/summer and that subsequent larvae underwent pelagic planktotrophic development.

Brittle star food consists of minute detrital particles and larger prey such as polychaetes and small crustaceans (Gosner 1979). Various shrimp and crab are proven predators of brittle stars (Pape-Lindstrom *et al.* 1996). Packer *et al.* (1994) indicated that American Plaice are major predators of *O. sarsi* in the Gulf of Maine. Brittle stars are also important prey items for numerous commercially significant shellfish and finfish species.

Relation to Man

Brittle stars can be used as indicators of human impact on the environment. To study the effects of contaminants using bioindicators, recolonisation patterns of soft-bottomed macrofauna, including *Ophiura affinis*, on defaunated copper spiked sediments were studied in a field experiment conducted in Norway (Olsgard 1999). The abundance and density of this brittle star species were significantly negatively correlated to increased sediment copper content. Bergmann and Moore (2001) and Bergmann *et al.* (2001; 2002) reported high (91%) post-trawling mortality rate of *O. ophiura* in the discards as determined from a trawl fishery off Scotland.

3.6.4 Sea Stars (*Asterias rubens; Leptasterias polaris; Solaster endeca*)

General Distributions

All three of these asteroid species occur in Newfoundland waters. With respect to their northwest Atlantic Ocean distributions, *Asterias rubens (*formerly *A. vulgaris)* occurs intertidally from Labrador south to Cape Cod. South of Cape Cod, this sea star occurs subtidally in waters as deep as 600 m. *Leptasterias polaris* is distributed from the Arctic south to New England. It is common in the intertidal zone at the northern part of its distribution, but southward it occurs progressively deeper in the subtidal zone (down to 105 m). *Solaster endeca* occurs from the Arctic to Cape Cod. It is common in the lower intertidal zone to the north, but is found in deeper water towards the southern end of its range (Gosner 1979). Sea stars tend to have a higher sensitivity to elevated water temperatures than to lowered water temperatures and upper and lower water temperature limits are about 15 to 17 °C and 0 to 2 °C, respectively (Marine Biological Association of the U.K., 2003). *A. rubens* can tolerate temperatures up to 25 °C (juveniles up to 27 °C), long exposure to air, and salinity levels less than 16 to 18 ppt (Barkhouse *et al.* 2007).

General Life Cycle of Asteroids

All asteroids have the ability to replace at least parts of their bodies following injury or natural autotomy by fission, a type of asexual reproduction. The following description pertains to the sexual reproduction of these animals.

Most asteroids are dioecious and fertilization occurs outside the animals in the surrounding seawater. There tends to be only one breeding season for most asteroids in temperate regions, usually during the spring (note: *L. polaris* is a winter spawner). During spawning, a female sea star might shed as many as 2.5 million eggs. In most asteroids, developing fertilized eggs and larval stages are planktonic (e.g., *A. rubens* , *S. endeca*) (Chia and Walker 1991).

There are two larval stages in non-brooding asteroids, bipinnariae and brachiolariae. While the larvae of *A. rubens* undergo pelagic planktotrophic development, the larvae of *S. endeca* undergo pelagic lecithotrophic development (Falk-Petersen 1982; Chia and Walker 1991; McEdward and Chia 1991).

In the non-brooding species, the initial larval stage is completely ciliated, but as development continues ciliation becomes confined to particular areas. Once arm formation occurs, the stage is known as a bipinnaria larva. Development time between fertilization and the bipinnaria larval stage can be several weeks. Asteroid larvae feed on phytoplankton and other fine suspended particles. The bipinnaria larvae become brachiolaria larvae with the development of three additional arms for settlement and attachment purposes. Settlement and attachment to the substrate precedes the complex metamorphosis to adult form and it is at this time that sea stars become fully epibenthic (Barnes 1980).

L. polaris is a dioecious brooding echinoderm. It broods its large lecithotrophic eggs and does not have pelagic larvae (Gosner 1979; Chia and Walker 1991). The reproductive cycle of *L. polaris* was examined over an 18-month period in the St. Lawrence Estuary (Boivin *et al.* 1986). There is a distinct annual cycle and the species consistently spawns in late fall-winter based on

water temperature. During the first year of the study, no brooding individuals were found during dives in July. They were initially detected in September and were common by October. During the second year of the study, brooding sea stars were not found until October and the peak did not occur until November. Such annual variations in gonadal production are common in marine invertebrates. Boivin *et al.* (1986) hypothesized that oogenesis in females of this species is a prolonged process and only a relatively small number of oocytes are spawned annually.

Under laboratory conditions, male *L. polaris* spawning was initiated once the water temperature fell to approximately 2 ° C and there were less than nine hours of daylight (Hamel and Mercier 1995). They observed the deposition of the negatively buoyant spermatozoa onto the substrate as a sticky film. The female, cued by the male activity, spawned onto the sperm layer. Time from fertilization to brachiolaria larvae was 40 days and fully developed young sea stars were apparent after 5 to 6 months post-fertilization.

Emerson (1973) reported that brooding by *L. polaris* in Logy Bay, Newfoundland begins in January. Water temperatures in the St. Lawrence Estuary in September are approximately 6 °C, but in Logy Bay the water does not drop to this temperature until late October. Spawning in this species involves behavioural changes such as aggregation of males and females and the search for suitable substrates (bedrock, boulders and cobble) for brooding (Hamel and Mercier 1995). Himmelman *et al.* (1982) reported that brooding *L. polaris* were abundant from February through May, but that numbers dwindled by June.

To protect the developing embryos, the female curves all of her six arms so that her body forms a protective cover over the young attached to the substrate. The only known brooding sea stars to attach their young to the substrate are in the *Leptasterias* genus (Himmelman *et al.* 1982). This species often broods in areas with considerable wave action. The female remains on her brood for 4 to 5 months and does not feed during this period (Emerson 1973). Brooding species produce far fewer larvae than those with pelagic planktotrophic or lecithotrophic larvae. Himmelman *et al.* (1982) reported that *L. polaris* weighing 100 to 200 g brood from 1,000 to 3,000 embryos. Brooding during the winter ensures that the young start their independent lives at the beginning of the period of elevated temperatures and abundant food.

Habitat and Feeding

The Boreal Asterias (*A. vulgaris*), the Polar Sea Star (*L. polaris*) and the Purple Sunstar (*S. endeca*) have been identified as key animal species in the biota assemblage associated with the "sea urchin barrens" habitat type characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. This habitat type typically has bedrock and/or boulder substrates, full salinity, some current effect and can withstand major ice scour (Hooper 1997). The degree of exposure to wave energy is typically moderate to high. The "sea urchin barrens" is one of the most abundant habitat types around the Newfoundland and Labrador coast (Hooper 1997). *A. rubens* can tolerate brackish water to salinities of 15 to 20 ppt. As with sea urchins, this sea star prefers water temperatures less than 15 °C. They are also common in rocky tide pools and near jetties/pilings, but may also occur on sandy or stony bottoms.

SCUBA surveys by Himmelman and Dutil (1991) in the northern Gulf of St. Lawrence found that *A. rubens* and *L. polaris* were the most abundant sea stars. Individuals measuring 1 to 5 cm

diameter were concentrated in the rocky subtidal zone, *A. vulgaris* being most concentrated in the depth range of 4 to 7 m and *L. polaris* most concentrated at depths $\leq$ 3 m. Adults of both species measuring 15 to 20 cm in diameter were associated with mixed and sediment substrates at greater depths. The few *S. endeca* individuals observed during the study were found in shallow and deep water on both soft sediment and rock substrates.

In the northern Gulf of St. Lawrence, these three sea star species are dominant predators with an important role in determining subtidal community structure (Himmelman 1991; Himmelman and Dutil 1991). *A. rubens* diet is dominated by molluscs, including Blue Mussels, Iceland Scallop and Waved Whelk. The only non-molluscan prey item that accounted for a substantial part of its diet was the Daisy Brittle Star (*Ophiopholis aculeata*) (Himmelman 1991). Himmelman and Steele (1971) did report that *A. vulgaris* also predated upon the Green Sea Urchin.

L. polaris feed almost exclusively on molluscs, including Blue Mussels, Arctic Surfclam (Rochette *et al.* 1995; Morissette and Himmelman 2000b), Iceland Cockle, Greenland Cockle, Iceland Scallop, Softshell Clam and Waved Whelk (Himmelman 1991). This sea star and the Waved Whelk are the most abundant carnivores in the northern Gulf of St. Lawrence (Jalbert *et al.* 1989) and both occur throughout the subtidal zone. Larger Polar Sea Stars are concentrated on soft substrates where they forage on large endobenthic bivalves and epibenthic gastropods. Morissette and Himmelman (2000b) described the interactions between *A. vulgaris* and *L. polaris* in a subtidal zone in the northern Gulf of St. Lawrence. *A. vulgaris* is considered a kleptoparasite that will move in on feeding *L. polaris* and steal food items. This behaviour can be detrimental or even lethal to *L. polaris*. However, the examination of the interactions between these two sea stars in deep water (6 m) mussel beds indicated that the shallow-water dominance of *A. vulgaris* is attenuated or that *L. polaris* may dominate in deeper areas (Gaymer and Himmelman 2002). The spatial and temporal variations in the use of habitat and prey resources by sea stars *A. vulgaris* and *L. polaris* were described by Gaymer *et al.* (2001a; b; 2002). The degree of overlap between these two sea stars varied between sites and appeared to be related to prey abundance, substrate type and slope. The general patterns observed included the aggregation of both species in shallow water and decreasing numbers with depth, showing inverse depth distributions and both species occurring in low numbers across the subtidal zone. They both preferred Blue Mussels as a food source, but below the mussel zone or after mussel patch decimation, a difference in diet became apparent. *A. vulgaris* switched to the ophiuroid *O. aculeata* and *L. polaris* fed primarily on the clam *Hiatella arctica*. Bégin *et al.* (2004) examined the distribution and diversity of invertebrate assemblages associated with macroalgal canopies in the northern Gulf of St. Lawrence and their effects on recruitment and growth of mussels.

Gagnon *et al.* (2003b) evaluated the impact of water motion and wave induced movement of kelp blades on movement of *A. vulgaris* towards Blue Mussels and its success in capturing its prey. Their observations supported the hypothesis that the kelp canopy in shallow water and the movement of the kelp blades provide mussels with a spatial refuge from sea star predation. They showed that a sea star can use distance chemodetection to localize prey under conditions of back-and-forth flow.

Naidu *et al.* (1999) discussed a catastrophic decline in Iceland Scallop abundance on the western Grand Banks of Newfoundland, possibly due to predation by various sea star species, including

L. polaris. Nadeau and Cliche (1998) described the effects of predation by sea stars (*L. polaris* and *A. rubens*) on juvenile Sea Scallops in the Gulf of St. Lawrence. The diet of *S. endeca* was dominated by echinoderms, including the Orange-Footed Sea Cucumber (*C. frondosa*) and Sand Dollars (*Echinarachnius parma*). Larger sunstars were also feeding on *L. polaris*. Wong and Barbeau (2003) investigated the effect of substrate on predation of juvenile Sea Scallops by *A. vulgaris* at two prey sizes and two prey densities under laboratory conditions. They found that substrate type (glass bottom, sand, granule, pebble) had a significant effect on the predation rate of the sea star on scallops. The predation rate and encounter rate with small scallops tended to decrease with increasing particle size, but substrate appeared to have no effect on the interactions between the sea stars and large scallops. Increased prey density also resulted in a higher predation rate and encounter rate between the sea stars and small scallops. The triggering of cannibalism in the sea star *A. vulgaris* due to declines in prey densities was reported by Witman *et al.* (2003) during their work in the southwest Gulf of Maine.

Relation to Man

Predation by *A. rubens* negatively impacts the Blue Mussel farming industry in Newfoundland. Studies of how to better predict sea star juvenile settlement, in relation to mussel spat settlement, will provide mussel growers with the ability to reduce the potential impact of this predatory sea star (Pryor and Parsons 1999; Pryor *et al.* 1999).

3.6.5 Sand Dollar (*Echinarachnius parma*)

General Distribution

This echinoid is a circumpolar species whose northwest Atlantic Ocean distribution extends from Labrador south to Cape Hatteras, North Carolina. It occurs mainly on sandy substrates from the shallow subtidal zone to depths greater than 800 m, but it may also occur in the lower intertidal zones of bays and beaches, especially in the northern part of its range. In the northwestern Atlantic Ocean, this burrowing echinoderm often occurs in great densities (100 species/m^2) and is a major factor in structuring soft bottom communities. According to Stanley and James (1971) with the exception of disturbance from storms, this species is the most important factor determining the composition of bottom communities on Sable Island Bank off Nova Scotia.

Life Cycle

Spawning and Fertilization: Unlike other echinoids, the males and females of *Echinarachnius parma* can be separated accurately on the basis of test shape (Hamel and Himmelman 1992). All echinoids are dioecious and their egg fertilization occurs externally in the water column. In temperate areas, spawning normally occurs in late spring/early summer (Barnes 1980).

Fertilized Eggs and Larvae: The blastula becomes ciliated and free-swimming within 12 hours after fertilization. The planktonic larval (echinopluteus larvae) period lasts 5 to 6 weeks (Barnes 1980). Pearce and Scheibling (1990) conducted laboratory experiments to examine induction of Sand Dollar echinopluteus larval settlement and metamorphosis by an adult-associated factor (chemical cue). These larvae do not attach upon settlement and metamorphosis occurs within 1 to 2 hours. Results showed that the larvae settle and metamorphose in significantly greater numbers on sand conditioned by adults than on various non-conditioned substrates. This

gregarious settlement is a possible response to adult produced chemical cues, which may contribute to the persistence of dense Sand Dollar beds and the aggregated distribution of the species.

Juveniles and Adults: This echinoderm species has been identified as a key animal species in the "clam bed" habitat type and the "scallop bed" habitat type characterized by Hooper (1997) as two classifications of marine coastal habitats in Newfoundland and Labrador. General physical characteristics typically associated with the clam bed habitat type includes fine to coarse sand/fine gravel substrates, full salinity and low to high exposure. Characteristics associated with the scallop bed habitat types include sand/fine gravel/shell gravel substrates and wide ranges of water temperature and exposure degree. Examples of the clam bed habitat in Newfoundland include Alexander Bay in Bonavista Bay, Shallow Bay in Gros Morne Park and The Tickle in Bonne Bay, while examples of the scallop bed habitat include Port au Port Bay, Salmonier Arm, Long Harbour in Fortune Bay, western Placentia Bay, Trinity Harbour, Harbour Buffett, Little Belle Island Shoal, Bonne Bay, Harbour Le Cou, shoals in the Strait of Belle Isle and offshore banks in the Labrador Current (Hooper 1997).

Preliminary studies on the ecology of Sand Dollars off the east coast of Newfoundland were conducted by Way (2002). The three study sites were all relatively sheltered and had water depths ranging from 7 to 10 m. In general, the substrates at all three locations were primarily composed of sand and all had algal films. The typical predatory species present at all locations included sea stars, crabs and sea urchins. *E. parma* was the dominant species, in terms of biomass, collected by epibenthic sled on a sandy bottom on the Grand Banks of Newfoundland at depths of 120 to 146 m (Prena *et al.* 1999; Kenchington *et al.* 2001).

In the northern Gulf of St. Lawrence, Cabanac and Himmelman (1996) examined the distribution and size structure of Sand Dollars on sediment slopes in the subtidal zone. During June to August, they found that large Sand Dollars (40 to 60 mm) predominated at depths < 4 m and smaller Sand Dollars (< 26 mm) were predominant in deeper water (4 to 24 m). These size classes might represent juveniles and adults. Cabanac and Himmelman (1996) proposed that there is shoreward movement by this species as individual size increases. Cabanac and Himmelman (1998) documented Sand Dollar movement in the field of up to 9.5 m over a 20-day period. Both small (20 to 30 mm diameter) and large (45 to 55 mm diameter) Sand Dollars tended to move upslope, but only the large ones showed a distinct preference for upstream movement in response to current. Based on results of laboratory experimentation, Highsmith and Emlet (1986) concluded that juvenile Sand Dollars developed from larvae that did not delay metamorphosis had higher growth rates and lower mortality rates. Total density of Sand Dollars increased with depth which was almost entirely attributable to juvenile animals (1-4 individuals/m^2 at 0.5-1.0 m depth to 740 individuals/m^2 at 20 m depth). The study also found that almost 95% of the juvenile Sand Dollars were buried compared to 30% of the adults. Water turbulence was substantially higher in shallow water than in the deeper areas (12-fold difference between 1 m and 24 m depths). The increased tendency of juveniles to bury themselves could also be an adaptation to avoid water turbulence. Therefore, juveniles may require a substrate which permits them to bury themselves, but does not shift during storms, potentially burying them too deeply.

Examinations of Sand Dollar gut contents have revealed sand grains, sponge spicules, echinoderm fragments, diatoms and detritus (Ghiold 1983). Sand Dollars occur frequently in the diets of some commercially and/or recreationally important fish species, including American Plaice and Yellowtail Flounder (Collie 1987; Steimle 1989; Bruno *et al.* 2000).

Relation to Man

Sand Dollars are important prey items for some commercially significant groundfish species. An assessment of the benthic environment following placer gold mining in the northeastern Bering Sea indicated that *E. parma* failed to recruit into mined areas, probably reflecting unconsolidated sediments, continued erosion of tailing piles and shoaling of dredge pits (Jewett *et al.* 1999). Chang *et al.* (1992) found *E. parma* to be one of the taxa consistently associated with minimally contaminated sediments in New York Bight.

3.7 BRYOZOA

3.7.1 Bryozoans (*Membranipora* spp.; *Alcyonidium* spp.)

Distributional Information

The occurrence and distribution of bryozoans are influenced primarily by the availability of suitable substrates. In favourable habitats, the diversity and ubiquity of bryozoan species might suggest that colony distribution is random. However, it has been shown that species are distributed according to varying tolerances to gross environmental parameters, microenvironmental characteristics and competitive interactions with other sessile organisms (Ryland and Hayward 1991). Bryozoan ecology is still an underdeveloped discipline and more work is required before the habitat requirements of individual species are understood (Ryland and Hayward 1991).

Two genera of bryozoans that occur in Newfoundland and Labrador include *Alcyonidium* and *Membranipora*. Both genera are algal epiphytic primarily on fully marine coasts (Ryland and Hayward 1991).

Most species of "rubbery bryozoans" (*Alcyonidium spp.*) are found along the entire northeast North American coast. *A. gelatinosum* is primarily boreal and *A. verrilli* occurs south of Cape Cod only. They generally occur from the lower intertidal to shallow subtidal depths (Gosner 1979). The only known free living Arctic bryozoan is *A. disciforme* (Kukliński and Porter 2004). It has a strictly Arctic circumpolar distribution. There is also a species that occurs in the Antarctic; *A. flabelliforme* (Porter and Hayward 2004).

The "lacy crusts" (*Membranipora spp.*) are described as encrusting bryozoans (Gosner 1979). These particular epiphytic genera of bryozoans have been identified as key organisms of the biota assemblage associated with the composite "kelp bed" habitat type characterized by Hooper (1997) as a type of marine coastal habitat in Newfoundland and Labrador. The typical substrate of this habitat type is hard bottom consisting of bedrock and/or boulders. These areas generally have high salinities and low temperatures and are mostly incompatible with significant ice scour (Hooper 1997). Hooper (1997) also subdivided "kelp bed" habitat based primarily on exposure; 1) low energy, 2) high energy, 3) fjord and 4) regular open coast.

General Life Cycle Information

Bryozoans are sessile and colonial animals, rarely longer than 0.5 mm and primarily hermaphroditic. Some species shed small eggs directly in the seawater. The larvae of these non-brooders are called cyphonautes (free-swimming, bivalve) larvae. These larvae are triangular, greatly compressed and have functional digestive tracts and ciliated food gathering apparatuses (Atkins 1955). They are active feeders and may persist as planktotrophic larvae for several months. Initially, these translucent larvae are positively phototactic, but they become less so as settlement approaches. The substrate surface is explored before attachment in order to find the proper surface texture, chemistry and/or presence of bacterial film. After the larvae attach to the substrate, they develop to the ancestrula stage, followed by continuous budding for community formation (Barnes 1980). Colonies of bryozoans are composed of numerous minute individual zooids that exhibit remarkable diversity in shape and function.

Most bryozoans are brooders in that they do not release gametes into the water column to complete external fertilization. Instead, fertilization, embryonic development and larval hatching occur within the animal. The larvae settle and metamorphose after a short free-swimming existence. Metamorphosis results in the transformation of the planktonic larvae into sessile, benthic juveniles that constitute the first zooids of the colony. Daughter zooids are subsequently produced by a budding process (Reed 1991). Both reproductive strategies apply to particular species of *Alcyonidium* and *Membranipora* (Ström 1977; Zimmer and Woollacott 1977).

Specific Information on *Alcyonidium* spp. and *Membranipora* spp.

Membranipora spp.: Water temperature and day length appear to be the primary exogenous factors controlling the timing of gametogenesis in bryozoans. Rising water temperatures and increasing durations of sunlight during the spring induce phytoplankton growth and, subsequently bryozoan reproduction. It has been observed in *Membranipora membranacea* growing on *Laminaria saccharina* that gametogenesis was initiated in regions of the colony where asexual growth was inhibited by contact with other colonies (i.e., density and composition of community). The simultaneously hermaphroditic zooids of *M. membranacea* colonies spawn gametes into the surrounding seawater. The fertilized eggs undergo planktotrophic development to form long-lived triangular cyphonaute larvae (Temkin 1994; Schwaninger 1999).

The larval stage of *M. membranacea* is generally planktonic for about 4 weeks (Yoshioka 1982), but may extend to 2 months. As with many benthic marine invertebrates, bryozoan larvae appear to exhibit distinct substrate preferences. The cyphonautes larvae of *M. membranacea* seem to prefer the younger, more proximal portions of blades of certain brown algae including *L. saccharina* (Brumbaugh *et al.* 1994). Experiments have indicated that cyphonautes larvae of *M. membranacea* are able to explore substrates in all directions in flow velocities that are much faster than their locomotion speeds (Abelson 1997). The preferential motion of these larvae appears to be upstream, perhaps enabling them to locate specific, obligatory settlement sites by tracking waterborne chemicals to their sources.

Metamorphosis in *Membranipora* spp. results in compound-composite ancestrulae (Reed 1991). After a short period of time (hours to days) each ancestrula buds (asexual reproduction) additional zooids to produce a colony (Hurlbut 1991).

In some epiphytic species that grow on transient substrates, growth and reproductive seasonality is correlated with that of their substrate. For example, at the Isle of Man, the annual growth and reproductive cycle of *M. membranacea* is correlated with that of the laminarians that it encrusts. Lambert *et al.* (1992) described the changes in the structure of a New England kelp bed caused by the introduction of *M. membranacea.* They concluded that the presence of this bryozoan on *Laminaria* spp. caused defoliation of the kelp bed by enhancing the susceptibility of the fronds to storm damage. Similarly, Levin *et al.* (2002) concluded that nonindigenous epiphytes such as *M. membranacea* can have detrimental effects on the structure of kelp beds off New Hampshire. There has been large scale defoliation of kelp beds associated with the presence of *M. membranacea* in Nova Scotia since the first reported occurrence in 1992 (Scheibling *et al.* 1999; Chapman *et al.* 2002). Recurrent kelp defoliation by *M. membranacea* could lead to important consequences to a number of species that use kelp beds as habitats for food, shelter and reproduction (Mann 2000). Scheibling and Gagnon (2006) showed the direct and indirect effects of *M. membranacea* on the structure and function of eastern Canada's shallow rocky ecosystems. They found that gaps within kelp beds similar to those resulting from defoliation by *M. membranacea* facilitate the establishment of the invasive green alga *Codium fragile* ssp. *tomentosoides* in Nova Scotia. Once established, *C. fragile* prevents recolonization by kelp and persists as the dominant canopy forming seaweed for prolonged periods. Saunders and Metaxas (2007) further showed strong positive relationship between thermal history of seawater and settlement pattern of *M. membranacea* on the kelp *S. longicruris* (formerly *Laminaria longicruris,* Lane *et al.* 2006) along the Atlantic coast of Nova Scotia.

There is evidence that *M. membranacea* can reduce spore output in the kelp *L. longicruris* as well as alter nitrogen and photosynthetic physiology in other kelp species (Saier and Chapman 2004; Hurd *et al.* 1994; 2000). Harvell *et al.* (1990) described the demography of *M. membranacea* in the field with an experimental manipulation of population density. They found that colonies of this bryozoan stopped growing upon contact with conspecifics.

Sagasti *et al.* (2000) examined the abundance and species composition of sessile and mobile epifaunal assemblages in a U.S. estuary with hypoxic episodes. They found that *Membranipora tenuis* was equally abundant in the areas with different oxygen levels.

Membranipora spp. are known epibionts of crabs (Patil and Anil 2000). Giri and Wicksten (2002) reported epibiotic growth of *Membranipora* spp. on shrimp collected off Texas in the Gulf of Mexico.

Okamura and Partridge (1999) demonstrated flow dependent morphology shifts by *M. membranacea.* Rapid water flows resulted in the miniaturization of colonies of this bryozoan. A decrease in growth rate in response to increased water flow rates has also been documented (Eckman and Duggins 1993).

Alcyonidium spp.: Colonies (gelatinous sheets) of some *Alcyonidium* species have hermaphrodite zooids, production of numerous eggs, embryonic development occurring in the water column and shelled feeding cyphonautes larvae (Temkin 1996).

Brooding species of *Alcyonidium* have slightly different reproductive methods. Hurlbut (1991) found that the colonies of *Alcyonidium polyoum* in New Hampshire contained embryos for most of the year and that ancestrulae occurred in very high numbers in early spring. Therefore, the colonies appeared to maintain a pool of brooded embryos throughout the winter and large numbers of larvae could be released within a short period of time. The peak in abundance of ancestrulae was followed by a peak in juvenile density, but not by an increase in adult density, indicating high juvenile mortality.

Hurlbut (1991) observed substrate selection by *A. polyoum* on rock, rockweed and Irish moss. The larvae of *A. polyoum* prefer to settle on the younger frond tips of the brown alga *Fucus serratus*. Their lifespan potentials are increased by settlement on ephemeral species and selection of the younger fronds should decrease competition for space (Ryland 1959; 1962).

McDermott (2001) described the symbiotic relationship between the Hermit Crab, *Pagurus longicarpus* and the bryozoan, *Alcyonidium albescens* in the waters off New Jersey. This same bryozoan is known to encrust Blue Crab in the North Carolina area (Winston and Key 1999; Key *et al.* 1999). Tanner Crab (*Chionoecetes bairdi*) in Alaska serve as substrate for various epibionts, including *Alcyonidium* spp. (Dick *et al.* 1998). Ryland and Porter (2000) described *A. reticulum*, a smooth surfaced species found encrusting intertidal stones and on *F. serratus* in south west Britain. Ryland (2001) also described another bryozoan, *Ascophyllum nodosum* that occurs on whelks off South Africa.

A. diaphanum was found to be widespread and abundant in the coastal waters of England and Wales (Porter *et al.* 2002). The rare intertidal locations where this bryozoan was found were characterized by tidal rapids or restrictions of outflowing or inflowing tidal streams coupled with a certain level of shelter from wave action. *A. diaphanum* was most abundant within a depth range of 10 to 30 m. Porter *et al.* (2001a) discussed the morphological aspects of this bryozoan species.

Alcyonidium gelatinosum was found in a saline lagoon along the south coast of England (Porter *et al.* 2001b; Porter 2004). The sheltered lagoon is characterized by weak tidal circulation, poor flushing, shallow water (< 1 m), predominantly mud substrate and seagrass. They found that *A. gelatinosum* occurring outside of the lagoon spawned in September-October, whereas the lagoonal bryozoans spawned in January-February.

General Prey/Predator Associations

Bryozoans feed on small microorganisms (e.g., bacteria, diatoms and other unicellular algae) that are trapped by the protrusible ciliated feeding tentacles. Grazing organisms including sea urchins, nudibranchs and certain fish species tend to be the primary predators of bryozoans. Primary competitors of bryozoans include sponges, algae and tunicates (Buchsbaum *et al.* 1987). Various phytoplankton probably provide the main food resource for bryozoan populations in nearshore waters. Studies have indicated that most of the food resource would come from phytoplankton under 50 µm in size (Winston 1977). Nielsen (2002) pointed out detailed morphological similarities between the ciliary bands of the feeding structures of adult *A. gelatinosum* and larval *Membranipor*a spp., suggesting that the feeding mechanisms are similar between the two bryozoan stages. Iyengar and Harvell (2002) indicated that *M. membranacea*

produces long, energetically costly spines in response to particular nudibranchs, which are predators of bryozoans.

Relation to Man

Bryozoans are sometimes considered nuisances because of their fouling tendencies. Colonies inhabiting the bottoms of ships, pilings, piers, docks, water intakes and other manmade structures are often referred to as foulants. On the other hand, bryozoans also produce a remarkable variety of chemical compounds, some of which are being investigated as beneficial compounds for man (Buchsbaum *et al.* 1987).

The effects of hydrocarbon contaminated substrates on recruitment of various fouling organisms were studied in the Gulf of Mexico (Banks and Brown 2002). Clay tiles exposed to crude oil were placed at two locations during two seasons at two tidal levels in an estuary. The recruitment of *M. savartii* was significantly reduced in all treatments.

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REFERENCES

Abbott R.T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold Co, New York.

Abelson, A. 1997. Settlement in flow: upstream exploration of substrata by weakly swimming larvae. Ecology 78(1): 160-166.

Abutrab, T. 1992. Food particle size preference of the sea anemone *Metridium senile*. Hons. Diss. (B.Sc.), Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 31 p.

Adams, N.L. 2001. UV radiation evokes negative phototaxis and covering behavior in the sea urchin *Strongylocentrotus droebachiensis*. Mar. Ecol. Prog. Ser. 213: 87-95.

Aiken, D.E. and S.L. Waddy. 1980. Reproductive biology. p. 215-276. *In* J.S. Cobb and B.F. Phillips (eds.). The biology and management of lobsters. Volume 2. Academic Press, New York, NY.

Aiken, D.E. and S.L. Waddy. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Can. J. Fish. Aquat. Sci. 43: 2258-2270.

Aiken, D.E., S.L. Waddy and S.M. Mercer. 2004. Confirmation of external fertilization in the American lobster, *Homarus americanus*. J. Crust. Biol. 24:474-480.

Aitken, A.E., Risk, M.J. and Howard, J.D. 1988. Animal-sediment relationships on a subarctic intertidal flat, Pangnirtung Fiord, Baffin Island, Canada. J. Sed. Petrol. 58(6): 969-978.

Alonso, M.K., Crespo, E.A., García, N.A. and Pedraza, S.N. 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. Environ. Biol. Fish. 63: 193-202.

Alyakrinskaya, I.O. 2003. Some ecological features of the lugworm *Arenicola marina* L. (Annelida, Polychaeta) and its morphological and biochemical adaptations to burrowing. Biol. Bull. 30(4): 411-418.

Amaratunga, T. and Rowell, T.W. 1988. Age and meat yield of Stimpson's surfclam, *Spisula polynyma*, a recently found commercial bivalve resource in eastern Canada. J. Shellfish. Res. 7(1): 107-108.

Amaratunga, T. and Rowell, T.W. 1986. New estimates of commercially harvestable biomass of Stimpson's surfclam, *Spisula polynyma*, on the Scotian Shelf based on the January through April 1986 test fishery and new age data. CAFSAC Res. Doc. 86/112. 24 p.

Ambrose, W.G., Jr. 1986. Estimate of removal rate of *Nereis virens* (Polychaeta: Nereidae) from an intertidal mudflat by gulls (*Larus* spp.). Mar. Biol. 90: 243-247.

Ambrose, W.G., Jr. 1991. Are infaunal predators important in structuring marine soft-bottom communities? Am. Zool. 31: 849–860.

Anderson, J.T. and Gardner, G.A. 1986. Plankton communities and physical oceanography observed on the Southeast Shoal region, Grand Bank of Newfoundland. J. Plankton Res. 8(6): 1111-1135.

Andresen, M. and Kristensen, E. 2002. The importance of bacteria and microalgae in the diet of the deposit-feeding polychaetes *Arenicola marina*. Ophelia 56(3): 179-196.

Andrews, S. 2000. The effect of fouling and current velocity on the feeding rate of the giant scallop, *Placopecten magellanicus*. Paper submitted for Advanced Diploma in Aquaculture, Marine Institute, St. John's, Newfoundland and Labrador.

Anger, K. 1984. Development and growth in larval and juvenile *Hyas coarctatus* (Decapoda, Majidae) reared in the laboratory. Mar. Ecol. Prog. Ser. 19: 115-123.

Anger, K. 1998. Patterns of growth and chemical composition in decapod crustacean larvae. Invertebr. Reprod. Dev. 33(2-3): 159-176.

Anthony, K.R.N. and Svane, I. 1994. Effects of flow-habitat on body size and reproductive patterns in the sea anemone *Metridium senile* in the Gullmarsfjord, Sweden. Mar. Ecol. Prog. Ser. 113: 257-269.

Appeldoorn, R.S. 1982. Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principal components analysis. Fish. Bull. 81(1): 75-84.

Arkhipkin, A.I. 2003. Towards identification of the ecological lifestyle in nektonic squid using statoliths morphometry. J. Molluscan Stud. 69: 171-178.

Arkhipkin, A.I. and Bjørke, H. 2000. Statolith shape and microstructure as indicators of ontogenetic shifts in the squid *Gonatus fabricii* (Oegopsida, Gonatidae) from the Norwegian Sea. Polar Biol. 23(1): 1-10.

Arai, M.N. 2001. Pelagic coelenterates and eutrophication: a review. Hydrobiologia 451: 69-87.

Arai, M.N., McFarlane, G.A., Saunders, M.W. and Mapstone, G.M. 1993. Spring abundance of medusae, ctenophores and siphonophores off southwest Vancouver Island: possible competition or predation on sablefish larvae. Can. Tech. Rep. Fish. Aquat. Sci. 1939. 37 p.

Armonies, W. 1992. Migratory rhythms of drifting juvenile molluscs in tidal waters of the Wadden Sea. Mar. Ecol. Prog. Ser. 83: 197-206.

Armonies, W. 2001. What an introduced species can tell you about the spatial extension of benthic species. Mar. Ecol. Prog. Ser. 209: 289-294.

Arsenault, D.J., Giasson, M.C. and Himmelman, J.H. 2000. Field examination of dispersion patterns of juvenile Iceland scallops (*Chlamys islandica*) in the northern Gulf of St. Lawrence. J. Mar. Biol. Assoc. U.K. 80: 501-508.

Arsenault, D.J., Girard, P. and Himmelman, J.H. 1997. Field evaluation of the effects of refuge use and current velocity on the growth of juvenile Iceland scallops, *Chlamys islandica* (O.F. Müller, 1776). J. Exp. Mar. Biol. Ecol. 217(1): 31-45

Arsenault, D.J. and Himmelman, J.H. 1996a. Ontogenic habitat shifts of the Iceland scallop, *Chlamys islandica* (Müller, 1776), in the northern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 53: 884-895.

Arsenault, D.J. and Himmelman, J.H. 1996b. Size-related changes in vulnerability to predators and spatial refuge use by juvenile Iceland scallops *Chlamys islandica*. Mar. Ecol. Prog. Ser. 140: 115-122.

Arsenault, D.J. and Himmelman, J.H. 1998a. Size-related decrease in spatial refuge use by Iceland scallops *Chlamys islandica*: ontogenetic behavioural changes or decreasing refuge availability? Mar. Ecol. Prog. Ser. 162: 153-161.

Arsenault, D.J. and Himmelman, J.H. 1998b. Spawning of the Iceland scallop (*Chlamys islandica* Müller, 1776) in the northern Gulf of St. Lawrence and its relationship to temperature and phytoplankton abundance. Veliger. 41(2): 180-185.

Arsenault, D.J. and Himmelman, J.H. 1998c. Size-related decrease in spatial refuge use by Iceland scallops *Chlamys islandica*: ontogenetic behavioural changes or decreasing refuge availability. Mar. Ecol. Prog. Ser. 162: 153-161.

Astthorsson, O.S. and Gislason, A. 1997. Biology of euphausiids in the subarctic waters north of Iceland. Mar. Biol. 129: 319-330.

Atkins, D. 1955. The cyphonautes larvae of the Plymouth area and the metamorphosis of *Membranipora membranacea* (L.). J. Mar. Biol. Assoc. U.K. 34: 441-449.

Avent, S.R., Bollens, S.M., Butler, M. Horgan, E. and Rountree, R. 2001. Planktonic hydroids on Georges Bank: ingestion and selection by predatory fishes. Deep Sea Res. (II Top. Stud. Oceanogr.) 48: 673-684.

Balch, T. and Scheibling, R.E. 2000. Temporal and spatial variability in settlement and recruitment of echinoderms in kelp beds and barrens in Nova Scotia. Mar. Ecol. Prog. Ser. 205: 139-154.

Balch, T., Hatcher, B.G. and Scheibling, R.E. 1999. A major settlement event associated with minor meteorologic and oceanographic fluctuations. Can. J. Zool. 77: 1657-1662.

Balser, E.J. 1998. Cloning by ophiuroid echinoderm larvae. Biol. Bull. 194(2): 187-193.

Båmstedt, U. 1990. Trophodynamics of the scyphomedusae *Aurelia aurita*: Predation rate in relation to abundance, size and type of prey. J. Plankton Res. 12: 215-229.

Båmstedt, U. and Karlson, K. 1998. Euphausiid predation on copepods in coastal waters of the Northeast Atlantic. Mar. Ecol. Prog. Ser. 172: 149-168.

Båmstedt, U., Wild, B. and Martinussen, M.B. 2001. Significance of food type for growth of ephyrae *Aurelia aurita* (Scyphozoa). Mar. Biol. 139: 641-650.

Banks, P.D. and Brown, K.M. 2002. Hydrocarbon effects on fouling assemblages of taxonomic differences, seasonal and tidal variation. Mar. Environ. Res. 53: 311-326.

Barbeau, M.A., Hatcher, B.G., Scheibling, R.E., Hennigar, A.W., Taylor, L.H. and Risk, A.C. 1996a. Dynamics of juvenile sea scallop (*Placopecten magellanicus*) and their predators in bottom seeding trials in Lunenburg Bay, Nova Scotia. Can. J. Fish. Aquat. Sci. 53: 2494-2512.

Barbeau, M.A., Scheibling, R.E., Hatcher, B.G., Taylor, L.H. and Hennigar, A.W. 1996b. Survival analysis of tethered juvenile sea scallops *Placopecten magellanicus* in field experiments: effects of predators, scallop size and density, site and season. Mar. Ecol. Prog. Ser. 115: 243-256.

Barker, K.M. and Chapman, A.O. 1990. Feeding preferences of periwinkles among four species of *Fucus*. Mar. Biol. 106: 113-118.

Barkhouse, C.L., Niles, M. and Davidson, L.-A. 2007. A literature review of sea star control methods for bottom and off bottom shellfish cultures. Can. Ind. Rep. Fish. Aquat. Sci. 279: vii + 38 p.

Barkman, J.J. 1955. On the distribution and ecology of *Littorina obtusata* (L.) and its specific units. Arch. Neerl. Zool. 11: 22-86.

Barnes, R.D. 1980. Invertebrate Biology (Fourth Edition). Saunders College/Holt, Rinehart and Winston, West Washington Square, Philadelphia, PA. 1089 p.

Barrett, R.T., Asheim, M. and Bakken, V. 1997. Ecological relationships between two sympatric congeneric species, common murres and thick-billed murres, *Uria aalge* and *U. lomvia*, breeding in the Barents Sea. Can. J. Zool. 75(4): 618-631.

Barrie, J. 1979. Diversity of marine benthic communities from nearshore environments on the Labrador and Newfoundland coasts. M.Sc. Thesis, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland. 85 p.

Barshaw, D.E. and Lavalli, K.L. 1988. Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, mud and rocks. Mar. Ecol. Prog. Ser. 48: 119-123.

Barsienėl, J., Lehtonen, K.K., Vuorinen, P.J., Lang, T., Pempkowiak, J., Syvokiene, J., Dedonyte, V., Rybakovas, A., Vuontisjärvi, H. and Kopecka, J. 2003. Biomarker responses in the mussel (*Mytilus edulis*) and the flounder (*Platichthys flesus*) in the Klaipeda-Butinge area (Baltic Sea). ICES CM 2003/M:11. 15 p.

Bayne, B.L. 1965. Growth and the delay of metamorphosis of the larvae of *Mytilus edulis* (L.). Ophelia 2(1): 1-47.

Bayne, B.L. 1976. The biology of mussel larvae. p. 81-120. *In* Bayne, B.L. (ed.). Marine mussels, their ecology and physiology. International Biological Programme: 10. Cambridge University Press, New York, NY.

Beal, F. and Kraus, M.G. 1991. Effects of intraspecific density on the survival of *Arctica islandica* (L.) within field enclosures located in eastern Maine. Abstracts: 1991 Annual Meeting, June 23-27, National Shellfisheries Association, Williamsburg, Virginia. 288 p.

Bégin, C., Johnson, L.E. and Himmelman, J.H. 2004. Macroalgal canopies: distribution and diversity of associated invertebrates and effects on the recruitment and growth of mussels. Mar. Ecol. Prog. Ser. 271: 121-132.

Behrends, G. and Schneider, G. 1995. Impact of *Aurelia aurita* medusae (Cnidaria, Scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). Mar. Ecol. Prog. Ser. 127: 39-45.

Beninger, P.G. 1987. A qualitative and quantitative study of the reproductive cycle of the giant scallop, *Placopecten magellanicus*, in the Bay of Fundy (New Brunswick, Canada). Can. J. Zool. 65: 495-498.

Bergeron, P. and Bourget, E. 1986. Shore topography and spatial partitioning of crevice refuges by sessile epibenthos in an ice disturbed environment. Mar. Ecol. Prog. Ser. 28: 129-145.

Bergmann, M., Beare, D.J. and Moore, P.G. 2001. Damage sustained by epibenthic invertebrates discarded in the Nephrops fishery of the Clyde Sea area, Scotland. J. Sea Res. 45(2): 105-118.

Bergmann, M. and Moore, P.G. 2001. Mortality of *Asterias rubens* and *Ophiura ophiura* discarded in the *Nephrops* fishery of the Clyde Sea area, Scotland. ICES J. Mar. Sci. 58: 531-542.

Bergmann, M., Wieczorek, S.K., Moore, P.G. and Atkinson, R.J.A. 2002. Utilisation of invertebrates discarded from the *Nephrops* fishery by variously selective benthic scavengers in the west of Scotland. Mar. Ecol. Prog. Ser. 233: 185-198.

Bergström, B.I., Gustavsson, A. and Strömberg, J.O. 1990. Determination of abundance of gelatinous plankton with a remotely operated vehicle (ROV). ICES CM 1990/L:77, Session V. 11 p.

Bergström, B. and Strömberg, J. 1997. Behavioural differences in relation to pycnoclines during vertical migration of the euphausiids *Meganyctiphanes norvegica* (M. Sars) and *Thysanoessa raschii* (M. Sars). J. Plankton Res. 19(2): 255-261.

Berkeley, A.A. 1930. The postembryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. Fish. 6(6): 79-163.

Berkes, F. 1976. Ecology of euphausiids in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33: 1894-1905.

Bertness, M.D. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology 65(2): 370-381.

Bertram, D.F. and Leggett, W.C. 1994. Predation risk during the early life history periods of fishes: separating the effects of size and age. Mar. Ecol. Prog. Ser. 109: 105-114.

Bertram, D.F. and Strathmann, R.R. 1998. Effects of maternal and larval nutrition on growth and form of planktonic larvae. Ecology 79(1): 315-327.

Beukema, J.J. and Dekker, R. 1995. Dynamics and growth of a recent invader into European coastal waters: the American razor clam, *Ensis directus*. J. Mar. Biol. Assoc. U.K. 75: 351-362.

Beukema, J.J., Dekker, R., Essink, K. and Michaelis, H. 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. Mar. Ecol. Prog. Ser. 211: 143-155.

Beukema, J.J., Essink, K. and Dekker, R. 2000. Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator-prey interactions. J. Anim. Ecology 69: 31-44.

Bigford, T.E. 1979. Synopsis of biological data on the rock crab *Cancer irroratus* Say. NOAA Tech. Rep. NMFS Circ. 426: 26 p.

Bjørke, H. 1995. Norwegian investigations on *Gonatus fabricii*. ICES CM/K:12. 13 p.

Bjørke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. Fish. Res. 52(1-2): 113-120.

Bjørke, H., Hansen, K. and Sundt, R.C. 1997. Egg masses of the squid *Gonatus fabricii* (Cephalopoda, Gonatidae) caught with pelagic trawl off northern Norway. Sarsia 82: 149-152.

Black, G.A.P., Mohn, R.K., Robert, G. and Tremblay, M.J. 1993. Atlas of the biology and distribution of the Sea scallop *Placopecten magellanicus* and Iceland scallop *Chlamys islandica* in the Northwest Atlantic. Can. Tech. Rep. Fish. Aquat. Sci. 1915. 34 p.

Black, G.A.P., Rowell, T.W. and Dawe, E.G. 1987. Atlas of the biology and distribution of the squids *Illex illecebrosus* and *Loligo pealeii* in the Northwest Atlantic. Can. Spec. Publ. Fish. Aquat. Sci. 100. 62 p.

Blackwell, B.F., Krohn, W.B. and Allen, R.B. 1995. Foods of nestling double-crested cormorants in Penobscot Bay, Maine, U.S.A.: Temporal and spatial comparisons. Colonial Waterbirds 18(2): 199-208.

Blaise, C., Gagné, F., Pellerin, J., Hansen, P.-D. and Trottier, S. 2002. Molluscan shellfish biomarker study of the Quebec, Canada, Saguenay Fjord with the softshell clam, *Mya arenaria*. Environ. Toxicol. 17: 170-186.

Boero, F. 1984. The ecology of marine hydroids and effects of environmental factors: a review. Mar. Ecol. (Berlin) 5: 93-118.

Boivin, Y., Larrivée, D. and Himmelman, J.H. 1986. Reproductive cycle of the subarctic brooding asteroid *Leptasterias polaris*. Mar. Biol. 92: 329-337.

Born, E.W., Rysgaard, S., Ehlmé, G., Sejr, M., Acquarone, M. and Leverman, N. 2003. Underwater observations of foraging free-living Atlantic walruses (*Odobenus rosmarus rosmarus)* and estimates of their food consumption. Polar Biol. 26: 348-357.

Bouchard, N., Pelletier, E. and Fournier, M. 1999. Effects of butyltin compounds on phagocytic activity of haemocytes from three marine bivalves. Environ. Toxicol. Chem. 18(3): 519-522.

Bourget, E. 1983. Seasonal variations of cold tolerance in intertidal molluscs and relation to environmental conditions in the St. Lawrence Estuary. Can. J. Zool. 61: 1193-1201.

Bourget, E., Ardisson, P.-L., Lapointe, L. and Daigle, G. 2003. Environmental factors as predictors of epibenthic assemblage biomass in the St. Lawrence system. Estuar. Coast. Shelf Sci. 57: 641-652.

Bourque, D., Miron, G. and Landry, T. 2001a. Predation on softshell clams (*Mya arenaria*) by the nemertean *Cerebratulus lacteus* in Atlantic Canada: implications for control measures. Hydrobiologia 456: 33-44.

Bourque, D., Miron, G., Landry, T. and MacNair, N.G. 2001b. Relationship between the nemertean *Cerebratulus lacteus* and the softshell clam, *Mya arenaria*: predator behaviour and prey selection. Can. Tech. Rep. Fish. Aquat. Sci. 2348. viii + 21 p.

Bourque, D., Miron, G. and Landry, T. 2002. Predator-prey relationship between the nemertean *Cerebratulus lacteus* and the softshell clam, *Mya arenaria*: surface-exploration activity and qualitative observations on feeding behaviour. Can. J. Zool. 80: 1204-1211.

Brady, S. M. and Scheibling, R. E. 2005. Repopulation of the shallow subtidal zone by green sea urchins (*Strongylocentotus droebachiensis*) following mass mortality in Nova Scotia, Canada. J. Mar. Biol. Assoc. U.K. 85: 1511-1517.

Brault, S. and Bourget, E. 1985. Structural changes in an estuarine subtidal epibenthic community: biotic and physical causes. Mar. Ecol. Prog. Ser. 21: 63-73.

Brenko, M. Hrs. and Calabrese, A. 1969. The combined effects of salinity and temperature on larvae of the mussel *Mytilus edulis*. Mar. Biol. 4: 224-226.

Brêthes, J.-C. F., Coulombe, F., Lafleur, P.-E. and Bouchard, R. 1987. Habitat and spatial distribution of early stages of the snow crab *Chionoecetes opilio* O. Fabricius off the north shore of the Gulf of St. Lawrence. J. Crust. Biol. 7(4): 667-681.

Brewer, R.H. 1991. Morphological differences between and reproductive isolation of two populations of the jellyfish *Cyanea* in Long Island, U.S.A. Hydrobiologia 216/217: 471-477.

Brey, T., Arntz, W.E., Pauly, D. and Rumohr, H. 1990. *Arctica (Cyprina) islandica* in Kiel Bay (Western Baltic): growth, production and ecological significance. J. Exp. Mar. Biol. Ecol. 136: 217-235.

Brillant, M.G.S. and MacDonald, B.A. 2002. Postingestive selection in the sea scallop (*Placopecten magellanicus*) on the basis of chemical properties of particles. Mar. Biol. 141: 457-465.

Brodeur, R.D., Sugisaki, H. and Hunt, G.L., Jr. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar. Ecol. Prog. Ser. 233: 89-103.

Brodziak, J. 1998. Revised biology and management of long-finned squid (*Loligo pealeii*) in the Northwest Atlantic. CalCOFI Rep. 39: 61-70.

Brodziak, J. and Hendrickson, L. 1999. An analysis of environmental effects on survey catches of squids *Loligo pealeii* and *Illex illecebrosus* in the northwest Atlantic. Fish. Bull. 97: 9-24.

Brodziak, J.K.T. and Macy, W.K., III. 1996. Growth of long-finned squid, *Loligo pealeii*, in the northwest Atlantic. Fish. Bull. 94(2): 212-236.

Brokordt, K.B., Guderley, H.E., Guay, M., Gaymer, C.F. and Himmelman, J.H. 2003. Sex differences in reproductive investment: maternal care reduces escape response capacity in the whelk *Buccinum undatum*. J. Exper. Mar. Biol. Ecol. 291(2): 161-180.

Brokordt, K.B., Himmelman, J.H. and Guderley, H.E. 2000. Effect of reproduction on escape responses and muscle metabolic capacities in the scallop *Chlamys islandica* Muller 1776. J. Exp. Mar. Biol. Ecol. 251(2): 205-225.

Brousseau, D.J. 1978. Spawning cycle, fecundity and recruitments in a population of softshell clam, *Mya arenaria*, from Cape Ann, Massachusetts. Fish. Bull. 76(1): 155-166.

Brousseau, D.J. and Baglivo, J.A. 1988. Life tables for two field populations of softshell clam, *Mya arenaria*, (Mollusca: Pelecypoda) from Long Island Sound. Fish. Bull. 86(3): 567-580.

Brown, R.G.B., Barker, S.P. and Gaskin, D.E. 1979. Daytime surface swarming by Meganyctiphanes norvegica (M. Sars) (Crustacea, Euphausiacea) off Brier Island. Bay of Fundy. Can. J. Zool. 57: 2285-2291.

Brumbaugh, D.R., West, J.M., Hintz, J.L. and Anderson, F.E. 1994. Determinants of recruitment by an epiphytic marine bryozoan: field manipulations of flow and host quality. p. 287-301. *In* Wilson, W.H., Jr., Stricker, S.A. and Shinn, G.L. (eds.). Reproduction and Development of Marine Invertebrates. The Johns Hopkins University Press, Baltimore, MD.

Bruno, I., Costas, G., Gonzalez, C. and Paz, X. 2000. Feeding chronology of yellowtail flounder (*Limanda ferruginea*) and American plaice (*Hippoglossoides platessoides*) on Grand Bank (NAFO Division 3N). Sci. Counc. Stud. NAFO 33: 103-116.

Bryant, A.D. and Hartnoll, R.G. 1995. Reproductive investment in two spider crabs with different breeding strategies. J. Exp. Mar. Biol. Ecol. 188: 261-275.

Bucklin, A. 1982. The annual cycle of sexual reproduction in the sea anemone *Metridium senile*. Can. J. Zool. 60: 3241-3248.

Bucklin A. 1987. Adaptive advantages of patterns of growth and asexual reproduction of the sea anemone *Metridium senile* (L.) in intertidal and submerged populations. J. Exp. Mar. Biol. Ecol. 110: 225-243.

Bulleri, F., Bertocci, I. and Micheli, F. 2002. Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. Mar. Ecol. Prog. Ser. 243: 101-109.

Burdett-Coutts, V. and Mextaxas, A. 2004. The effect of the quality of food patches on larval vertical distribution of the sea urchins *Lytechinus variegatus* (Lamarck) and *Strongylocentrotus droebachiensis* (Mueller). J. Exp. Mar. Biol. Ecol. 308(2): 221-236.

Buresch, K.C., Boal, J.G., Nagle, G.T., Knowles, J., Nobuhara, R., Sweeney, K. and Hanlon, R.T. 2004. Experimental evidence that ovary and ividucal gland extracts influence male agonistic behavior in squids. Biol. Bull. 206(1): 1-3.

Burke, M.V. and Mann, K.H. 1974. Productivity and production: biomass ratios of bivalve and gastropod populations in an eastern Canadian estuary. J. Fish. Res. Board Can. 31: 167-177.

Burrows, M.T., Moore, J.J. and James, B. 2002. Spatial synchrony of population changes in rocky shore communities in Shetland. Mar. Ecol. Prog. Ser. 240: 39-48.

Burton, C.A. 2001. The role of lobster (*Homarus* spp.) hatcheries in ranching, restoration and remediation programmes. Hydrobiologia 465: 45-48.

Buschbaum, C. 2002. Predation on barnacles of intertidal and subtidal mussel beds in the Wadden Sea. Helgol. Mar. Res. 56: 37-43.

Buchsbaum, R., Buchsbaum, M., Pearse, J. and Pearse, V. 1987. Animals without backbones. 3rd edition. University of Chicago Press, Chicago.

Buschbaum, C. and Reise, K. 1999. Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.). Helgol. Mar. Res. 53: 56-61.

Bustnes, J.O. 1998. Selection of blue mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*, by size in relation to shell content. Can. J. Zool. 76: 1787-1790.

Bustos-Baez, S. and Frid, C. 2003. Using indicator species to assess the state of macrobenthic communities. Hydrobiologia 496: 299-309.

Cabanac, A. and Himmelman, J.H. 1996. Population structure of the sand dollar *Echinarachnius parma* in the subtidal zone of the northern Gulf of St. Lawrence, eastern Canada. Can. J. Zool. 74: 698-709.

Cabanac, A. and Himmelman, J.H. 1998. Directional movement of the sand dollar *Echinarachnius parma*. Ophelia 48(2): 93-102.

Caddy, J.F., Chandler, R.A. and Wilder, D.G. 1974. Biology and commercial potential of several underexploited molluscs and crustaceans on the Atlantic coast of Canada. A paper presented to the Federal-Provincial Committee on Utilization of Atlantic Resources. Montreal, February 1974. 111 p.

Caddy, J.F., Chandler, R.A. and Wilder, D.G. 1977. Biology and commercial potential of several underexploited species of shellfish and crustacea on the Atlantic coast of Canada. Fisheries and Marine Service, Biological Station, St. Andrews, N.B. 93 p.

CAFID (Canada/Newfoundland Co-operation Agreement for Fishing Industry Development). 1996. Experimental whelk fishing: Conception Bay, 1996. 4 p.

Calder, D.R. 1990. Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, U.S.A. Can. J. Zool. 68: 442-450.

Campbell, A. 1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, Eastern Canada. Can. J. Fish. Aquat. Sci. 43: 2197-2205.

Campbell, A. 1989. Dispersal of American lobsters, *Homarus americanus*, tagged off southern Nova Scotia. Can. J. Fish. Aquat. Sci. 46(11): 1842-1844.

Campbell, A. and Stasko, A.B. 1985. Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 42: 229-238.

Campbell, A. and Stasko, A.B. 1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy. Mar. Biol. 92: 393-404.

Camus, L., Jones, M.B., Borseth, J.F., Regoli, F. and Depledge, M.H. 2002. Heart rate, respiration and total oxyradical scavenging capacity of the Arctic spider crab, *Hyas araneus*, following exposure to polycyclic aromatic compounds via sediment and injection. Aquat. Toxicol. 61(1-2): 1-13.

Cargnelli, L.M., Griesbach, S.J., Packer, D.B. and Weissberger, E. 1999a. Essential fish habitat source document: Ocean quahog, *Arctica islandica*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-148. 11 p.

Cargnelli, L.M., Griesbach, S.J., Packer, D.B. and Weissberger, E. 1999b. Essential fish habitat source document: Atlantic surfclam, *Spisula solidissima*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-142. 13 p.

Cargnelli, L.M., S.J. Griesbach and C.A. Zetlin. 1999c. Essential fish habitat source document: Northern shortfin squid, Illex illecebrosus, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-147. 21 p.

Cargnelli, L.M., Griesbach, S.J., McBride, C., Zetlin, C.A. and Morse, W.W. 1999d. Essential fish habitat source document: Longfin inshore squid, *Loligo pealeii*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-146. 16 p.

Caron, A., Boucher, L., Desrosiers, G. and Retière, C. 1995. Population dynamics of the polychaete *Nephtys caeca* in an intertidal estuarine environment (Quebec, Canada). J. Mar. Biol. Assoc. U.K. 75: 871-884.

Caron, A., Desrosiers, G., Miron, G. and Retière, C. 1996. Comparison of spatial overlap between the polychaetes *Nereis virens* and *Nephtys caeca* in two intertidal estuarine environments. Mar. Biol. 124: 537-550.

Caron, A., Desrosiers, G., Olive, P.J.W., Retière, C. and Nozais, C. 2004. Comparison of diet and feeding activity of two polychaetes, *Nephtys caeca* (Fabricius) and *Nereis virens* (Sars), in an estuarine intertidal environment in Quebec, Canada. J. Exp. Mar. Biol. Ecol. 304(2): 225-242.

Caron, A., Desrosiers, G., Retière, C. and Hudier, E. 1993. Comparaison démographique des populations de deux annélides polychètes selon l'orientation des baies dans l'estuaire du Saint-Laurent. Oceanol. Acta. 16(4): 403-412.

Carrington, E. 2002. Seasonal variation in the attachment strength of blue mussels: causes and consequences. Limnol. Oceanogr. 47(6): 1723-1733.

Carscadden, J.E., Frank, K.T. and Miller, D.S. 1989. Capelin (*Mallotus villosus*) spawning on the Southeast Shoal: influence of physical factors past and present. Can. J. Fish. Aquat. Sci. 46: 1743-1754.

Carter, J.A. and Steele, D.H. 1981. Attraction to and selection of prey by immature lobsters (*Homarus americanus*). Can. J. Zool. 60: 326-336.

Carter, J.A. and Steele, D.H. 1982. Stomach contents of immature lobsters (*Homarus americanus)* from Placentia Bay, Newfoundland. Can. J. Zool. 60: 337-347.

Catto, N.R., R.G. Hooper, M.R. Anderson, D.A. Scruton, J.D. Meade, L.M.N. Ollerhead and U.P Williams. 1999. Biological and geomorphological classification of Placentia Bay: a preliminary assessment. Can. Tech. Rep. Fish. Aquat. Sci. 2289: v + 35 p.

Cerrato, R.M. and Keith, D.L. 1992. Age, structure, growth and morphometric variations in the Atlantic surfclam, *Spisula solidissima*, from estuarine and inshore waters. Mar. Biol. 114: 581-593.

Chandler, R.A., Robinson, S.M.C. and Martin, J.D. 2001. Collection of softshell clam (*Mya arenaria* L.) spat with artificial substrates. Can. Tech. Rep. Fish. Aquat. Sci. 2390. iii + 8 p.

Chang, S., Steimle, F.W., Reid, R.N., Fromm, S.A., Zdanowicz, V.S. and Pikanowski, R.A. 1992. Association of benthic macrofauna with habitat types and quality in the New York Bight. Mar. Ecol. Prog. Ser. 89: 237-251.

Chapman, A.S., Scheibling, R.E., Chapman, A.R.O., 2002. Species introductions and changes in marine vegetation of Atlantic Canada. p. 133-148. *In* Claudi, R., Nantel, P. and Muckle-Jeffs, E. (eds.), Alien Invaders in Canada's Waters, Wetlands and Forests. Natural Resources Canada, Canadian Forest Service Science Branch, Ottawa.

Charmantier, G., Charmantier-Daures, M. and Aiken, D.E. 1991. Metamorphosis in the lobster *Homarus* (Decapoda): A review. J. Crust. Biol. 11(4): 481-495.

Charmantier, G., Haond, C., Lignot, J.-H. and Charmantier-Daures, M. 2001. Ecophysiological adaptation to salinity throughout a life cycle: a review in homarid lobsters. J. Exp. Biol. 204: 967-977.

Chase, M.E. and Thomas, M.L.H. 1995. The effect of the rate and onset of temperature increase on spawning of the periwinkle, *Littorina littorea* (L.). J. Exp. Mar. Biol. Ecol. 186: 277-287.

Chia, F.S. and Walker, C.W. 1991. Echinodermata: Asteroidea. p. 301–353. *In* Giese, A.C., Pearse, J.S. and Pearse, V.B. (eds.). Reproduction of Marine Invertebrates, Volume VI: Echinoderms and Lophophorates. Boxwood Press, Pacific Grove, CA.

Chintala, M.M. and Grassle, J.P. 1995. Early gametogenesis and spawning in "juvenile" Atlantic surfclams *Spisula solidissima* (Dillwyn, 1819). J. Shellfish Res. 14(2): 301-306.

Chintala, M.M. and Grassle, J.P. 2001. Comparison of recruitment frequency and growth of surfclams, *Spisula solidissima* (Dillwyn, 1817), in different inner-shelf habitats of New Jersey. J. Shellfish Res. 20(3): 1177-1186.

Chou, C.L., Paon, L.A. and Moffatt, J.D. 2002a. Metal contaminants for modeling lobster (*Homarus americanus*) migration patterns in the Inner Bay of Fundy, Atlantic Canada. Mar. Poll. Bull. 44: 134-141.

Chou, C.L., Paon, L.A. and Moffatt, J.D. 2002b. Cadmium, copper, manganese, silver and zinc in rock crab (*Cancer irroratus*) from highly copper contaminated sites in the Inner Bay of Fundy, Atlantic Canada. Bull. Environ. Contam. Toxicol. 68: 885-892.

Chou, C.L., Paon, L.A., Moffatt, J.D. and Zwicker, B. 2003a. Bioaccumulation and interrelationship of manganese and zinc in horse mussel *Modiolus modiolus* from Eastern Canada. Fish. Sci. 69(2): 369-378.

Chou, C.L., Paon, L.A., Moffatt, J.D. and King, T. 2003b. Selection of bioindicators for monitoring marine environmental quality in the Bay of Fundy, Atlantic Canada. Mar. Poll. Bull. 46: 756-762.

Christian, J.R. 1995. Patterns of diel activity and movements of the American lobster, *Homarus americanus*, as determined by ultrasonic telemetry. M.Sc. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland. 110 p.

Clancy, M. and Cobb, J.S. 1995. Rock crab recruitment: Is there evidence for a "novel" strategy? Twenty-Third Benthic Ecology Meeting, New Brunswick, New Jersey, 17-19 March, 1995. Abstract.

Clancy, M. and Cobb, J.S. 1997. Effect of wind and tidal advection on distribution patterns of rock crab *Cancer irroratus* megalopae in Block Island Sound, Rhode Island. Mar. Ecol. Prog. Ser. 152: 217-225.

Clarke, A.P., Mill, P.J. and Grahame, J. 2000. The nature of heat coma in *Littorina littorea* (Mollusca: Gastropoda). Mar. Biol. 137: 447-451.

Coady, L.W. 1973. Aspects of the reproductive biology of *Cucumaria frondosa* (Gunnerus, 1770) and *Psolus fabricii* (Düben and Koren, 1846) (Echinodermata: Holothuroidea) in shallow waters of the Avalon Peninsula, Newfoundland. M.Sc. Thesis, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland. 117 p.

Coelho, M.L. 1985. Review of the influence of oceanographic factors on cephalopod distribution and life cycles. Sci. Counc. Stud. NAFO 9: 47-57.

Colbourne, E.B., Dawe, E.G., Parsons, D.G., Murphy, E.F., Bowering, W.R., Dalley, E.L. Anderson, J.T., Dempson, J.B., Orr, D., Stansbury, D.E. and Ennis, G.P. 2002. A preliminary review of environmental-stock relationships for some species of marine organisms in NAFO waters of the Northwest Atlantic. Sci. Counc. Res. Doc. NAFO 02/34. 21 p.

Colbourne, E.B. and Orr, D.C. 2003. The distribution and abundance of northern shrimp (*Pandalus borealis*) in relation to bottom temperatures in NAFO Divisions 3LNO based on multi-species surveys from 1995-2003. Sci. Counc. Res. Doc. NAFO 03/81. 18 p.

Collie, J.S. 1987. Food selection by yellowtail flounder (*Limanda ferruginea*) on Georges Bank. Can. J. Fish. Aquat. Sci. 44: 357-367.

Collie, J.S., Escanero, G.A. and Valentine, P.C. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. Mar. Ecol. Prog. Ser. 155: 159-172.

Comeau, M., Conan, G.Y., Maynou, F., Robichaud, G., Therriault, J.-C. and Starr, M. 1998. Growth, spatial distribution and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 55: 262-279.

Comeau, M. and Savoie, F. 2002. Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. Fish. Bull. 100: 181-192.

Comeau, M., Starr, M., Conan, G.Y., Robichaud, G. and Therriault, J.-C. 1999. Fecundity and duration of egg incubation for multiparous female snow crabs (*Chionoecetes opilio*) in the fjord of Bonne Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 56: 1088-1095.

Coon, S.L., Bonar, D.B. and Weiner, R.M. 1985. Induction of settlement and metamorphosis of the Pacific oyster, *Crassostrea gigas*, by L-dopa and catecholamines. J. Exp. Mar. Biol. Ecol. 94: 211-221.

Corey, S. 1980. The life history of *Crangon septemspinosa* Say (Decapoda, Caridea) in the shallow sublittoral area of Passamaquoddy Bay, New Brunswick, Canada. Crustaceana 41(1): 21-28.

Corey, S. 1987. Reproductive strategies and comparative fecundity of *Crangon septemspinosa* Say (Decapoda, Caridea). Crustaceana 52(1): 25-28.

Cornelius, P.F.S. 1995. North-West European thecate hydroids and their medusae. Part 2. Sertulariidae to Campanulariidae. p. 296-300. *In* Barnes, R.S.K and Crothers, J.H. (eds.). Synopses of the British fauna (new seris). Field Studies Council, Shrewsbury.

Costello, J.H. and Colin, S.P. 1994. Morphology, fluid motion and predation by the scyphomedusa *Aurelia aurita*. Mar. Biol. 121: 327-334.

Costello, D.P. and Henley, C. 1971. Methods for obtaining and handling marine eggs and embryos. Mar. Biol. Lab. (Woods Hole). xvii + 247 p.

Couturier, C., Dabinett, P. and Lanteigne, M. 1995. Scallop culture in Atlantic Canada. p. 297-340. *In* Boghen, A.D. (ed.). Cold-water Aquaculture in Atlantic Canada. The Canadian Institute for Research on Regional Development. Sackville, NB.

Cowan, D. 1999. Method for assessing relative abundance, size distribution and growth of recently settled and early juvenile lobsters (*Homarus americanus*) in the lower intertidal zone. J. Crust. Biol. 19(4): 738-751.

Cranford, P.J. and Grant, J. 1990. Particle clearance and absorption of phytoplankton and detritus by the sea scallop *Placopecten magellanicus* (Gmelin). J. Exp. Mar. Biol. Ecol. 137: 105-121.

Cranford, P.J. and Gordon, D.C., Jr. 1992. The influence of dilute clay suspensions on sea scallop (*Placopecten magellanicus*) feeding activity and tissue growth. Neth. J. Sea Res. 30: 107-120.

Crawford, R.E. 1992. Biology of the Iceland scallop and some implications for management of an Arctic fishery. Can. Manuscr. Rep. Fish. Aquat. Sci. 2175. 11 p.

Creaser, E.P. and Clifford, D.A. 1982. Life history studies of the sandworm, *Nereis virens* Sars, in the Sheepscot Estuary, Maine. Fish. Bull. 80(4): 735-743.

Cross, W.E. and Thomson, D.H. 1987. Effects of experimental releases of oil and dispersed oil on Arctic nearshore macrobenthos. Arctic 40 (suppl. 1): 184-200.

Culliney, J.L. 1974. Larval development of the giant scallop *Placopecten magellanicus* (Gmelin). Biol. Bull. 147: 321-332.

Cummins, V., Coughlan, S., McClean, O., Connolly, N., Mercer, J. and Burnell, G. 2002. An assessment of the potential for the sustainable development of the edible periwinkle, *Littorina littorea*, industry in Ireland. Report for the Marine Research Measure (Operational Programme for Fisheries 1994-1999). xiii + 85 p.

Cuthbert, F.M., Hooper, R.G. and McKeever, T. 1995. Sea urchin feeding and ranching experiments. Report for Canadian Centre for Fisheries Innovation. Project Report: AUI-503. 54 p.

Cuthbert, F.M., Hooper, R.G. and McKeever, T. 1996. Addendum to Sea urchin aquaculture-Phase II: Ration size, seasonal growth rates, mixed kelp diets, fish diet, old urchin growth and baiting confinement experiments. 37 p.

Cuzin-Roudy, J. 2000. Seasonal reproduction, multiple spawning and fecundity in northern krill, *Meganyctiphanes norvegica* and Antarctic krill, *Euphausia superba*. Can. J. Fish. Aquat. Sci. 57(Suppl. 3): 6-15.

Cuzin-Roudy, J., Tarling, G.A. and Strömberg, J.-O. 2004. Life cycle strategies of Northern krill (*Meganyctiphanes norvegica*) for regulating growth, moult and reproductive activity in various environments: the case of fjordic populations. ICES J. Mar. Sci. 61: 721-737.

Dalley, E.L. Anderson, J.T. and Davis, D.J. 1999. Plankton and nekton of the Northeast Shelf and Grand Banks in 1998. DFO CSAS Res. Doc. 99/142. 37 p.

Dalpadado, P. and Bogstad, B. 2004. Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biol. 27: 140-154.

Dalpadado, P., Ellertsen, B., Melle, W. and Skjoldal, H.R. 1998a. Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic Seas. Sarsia 83: 103-116.

Dalpadado, P., Ellertsen, B., Melle, W. and Dommasnes, A. 1998b. Food and feeding conditions and prey selectivity of herring (*Clupea harengus*) through its feeding migrations from coastal areas of Norway to the Atlantic and Arctic watermasses of the Nordic Seas. ICES CM 1998/R:2. 28 p.

Dalpadado, P., Ellertsen, B., Melle, W. and Dommasnes, A. 2000. Food and feeding conditions of Norwegian spring-spawning herring (*Clupea harengus*) through its feeding migrations. ICES J. Mar. Sci. 57(4): 843-857.

Dalpadado, P., Melle, W., Ellertsen, B. and Dommasnes, A. 1996. Food and feeding conditions of herring (*Clupea harengus*) in the Norwegian Sea. ICES CM 1996/L:20. 25 p.

Dalpadado, P. and Skjoldal, H.R. 1996. Abundance, maturity and growth of the krill species *Thysanoessa inermis* and *T. longicaudata* in the Barents Sea. Mar. Ecol. Prog. Ser. 144: 175-183.

Daly, J.M. 1978a. The annual cycle and the short term periodicity of breeding in a Northumberland population of *Spirorbis spirorbis* (Polychaeta: Serpulidae). J. Mar. Biol. Assoc. U.K. 58: 161-176.

Daly, J.M. 1978b. Growth and fecundity in a Northumberland population of *Spirorbis spirorbis* (Polychaeta: Serpulidae). J. Mar. Biol. Assoc. U.K. 58: 177-190.

Davidson, K.G. and Chin, E.A. 1991. A comparison of the taxonomic characteristics and duration of the laboratory reared larvae of snow crabs, *Chionoecetes opilio* (O. Fabricius) and toad crabs, (*Hyas* sp.) from Atlantic Canada. Can. Tech. Rep. Fish. Aquat. Sci. 1762. 21 p.

Davies, M.S. and Beckwith, P. 1999. Role of mucus trails and trail-following in the behaviour and nutrition of the periwinkle *Littorina littorea*. Mar. Ecol. Prog. Ser. 179: 247-257.

Davis, C.V. 1999. Juvenile growth of cage-reared Stimpson's surfclams (*Mactromeris polynyma*) in Maine, U.S.A. Annual Meeting of the National Shellfish Association, June 1999. Abstract: J. Shellfish Res. 18(1).

Davis, C.V. and Shumway, S.E. 1996. Larval and juvenile growth of Stimpson's surfclam-a new candidate species for aquaculture development? Annual Meeting of the National Shellfish Association, April 1996. Abstract: J. Shellfish Res. 15(2): 479-480.

Dawe, E.G. 1999. Migration patterns of short-finned squid and fishery effects inferred from research survey and fishery data. Sci. Counc. Res. Doc. NAFO 99/49. 11 p.

Dawe, E.G. and Beck, P.C. 1997. Population structure, growth and sexual maturation of short-finned squid (*Illex illecebrosus*) at Newfoundland. Can. J. Fish. Aquat. Sci. 54: 137-146.

Dawe, E.G., Colbourne, E.B. and Drinkwater, K.F. 2000. Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). ICES J. Mar. Sci. 57: 1002-1013.

Dawe, E.G., Colbourne, E.B. and Drinkwater, K.F. 1998a. Environmental effects on short-finned squid recruitment to Canadian fishing areas. Sci. Counc. Res. Doc. NAFO 98/54. 14 p.

Dawe, E.G., Bowering, W.R. and Joy, J.B. 1998b. Predominance of squid (*Gonatus* spp.) in the diet of Greenland halibut (*Reinhardtius hippoglossoides*) on the deep slope of the northeast Newfoundland continental shelf. Fish. Res. 36: 267-273.

Dawe, E.G., Dalley, E.L. and Lidster, W.W. 1997. Fish prey spectrum of short-finned squid (*Illex illecebrosus*) at Newfoundland. Can. J. Fish. Aquat. Sci. 54 (Suppl. 1): 200-208.

Dawe, E.G., Drew, H.J., Veitch, P.J., Seward, E. and Beck, P.C. 2003. An assessment of the Newfoundland and Labrador snow crab in 2002. Can. Sci. Adv. Secret. Res. Doc. 2003/025.

Dawe, E.G. and Hendrickson, L.C. 1998. A review of the biology, population dynamics and exploitation of short-finned squid in the northwest Atlantic Ocean, in relation to assessment and management of the resource. Sci. Counc. Res. Doc. NAFO 98/59. 33 p.

Dawe, E.G., Hendrickson, L.C., Colbourne, E.B., Drinkwater, K.F, and M.A. Showell. 2007. Ocean climate effects on the relative abundance of short-finned (*Illex illecebrosus)* and long-finned (*Loligo pealeii*) squid in the northwest Atlantic Ocean. Fish. Oceanogr. 16(4): 303-316.

Dawe, E.G., Hendrickson, L.C., Colbourne, E.B., Showell, M.A., Drinkwater, K.F., Jones, D.D. and Methven, D.A. 2002. Environmental regulation of the relative abundance of two squid species in the Northwest Atlantic Ocean, *Illex illecebrosus* and *Loligo pealeii*. Sci. Counc. Res. Doc. NAFO 02/40. 16 p.

Dawe, E.G., Hendrickson, L.C., Colbourne, E.B., Showell, M.A., Jones, D.D. and Methven, D.A. 2001. Squids as potential indicator species of environmental or ecosystem change in the Northwest Atlantic Ocean. ICES CM 2001/K:07.

Dawe, E.G., Shears, J.C., Balch, N.E. and O'Dor, R.K. 1990. Occurrence, size and sexual maturity of long-finned squid (*Loligo pealeii*) at Nova Scotia and Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 47: 1830-1835.

De Lafontaine, Y. and Leggett, W.C. 1988. Predation by jellyfish on larval fish: an experimental evaluation employing in situ enclosures. Can. J. Fish. Aquat. Sci. 45: 1173-1190.

De Schweinitz, E.H. and Lutz, R.A. 1976. Larval development of the northern horse mussel *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. Biol. Bull. 150: 348-360.

Dean, D., Chapman, S.R. and Chapman, C.S. 1987. Reproduction and development of the sabellid ploychaete *Myxicola infundibulum*. J. Mar Biol. Assoc. U.K. 67: 431-439.

Degraer, S., Mouton, I., De Neve, L. and Vincx, M. 1999. Community structure and intertidal zonation of the macrobenthos on a macrotidal, ultra-dissipative sandy beach: summer-winter comparison. Estuaries 22(3B): 742-752.

Desrosiers, G., Caron, A., Olivier, M. and Miron, G. 1994. Cycle de développement d'une population intertidale de *Nereis virens* (Polychaeta Nereidae) de l'estuaire maritime du Saint-Laurent. Oceanol. Acta. 17(6): 683-695.

Desrosiers, R.R., Désilets, J. and Dubé, F. 1996. Early developmental events following fertilization in the giant scallop *Placopecten magellanicus*. Can. J. Fish. Aquat. Sci. 53: 1382-1392.

DFA (Department of Fisheries and Aquaculture, Government of Newfoundland and Labrador). 2006. Newfoundland Aquaculture Fact Sheet.

DFO. 1988. Underwater World: The Sea Scallop. Communications Directorate, Ottawa, ON. 8 p.

DFO. 1989a. Underwater World: Atlantic Shellfish. Communications Directorate, Ottawa, ON. 7 p.

DFO. 1989b. Underwater World: Crabs of the Atlantic Coast of Canada. Communications Directorate, DFO, Ottawa, ON. 8 p.

DFO. 1993a. Underwater World: Softshell Clam. Communications Directorate, Ottawa, ON. 6 p.

DFO. 1993b. Underwater World: The Northern Shrimp. Communications Directorate, Ottawat, ON. 6 p.

DFO. 1996a. Scotian Shelf Atlantic Surfclam. DFO Atl. Fish. Stock Status Rep. 96/122E. 2 p.

DFO. 1996b. Southern Gulf bar clam. DFO Atl. Fish. Stock Status Rep. 96/100E. 3 p.

DFO. 1996c. Coastal Zone Species Profile Series No. 6: Soft Shell Clam. 2 p.

DFO. 1996d. Coastal Zone Species Profile Series No. 7: Blue Mussel. 2 p.

DFO. 1996e. Coastal Zone Species Profile Series No. 5: Deep Sea Scallop. 2 p.

DFO. 1996f. Coastal Zone Species Profile Series No. 1: American Lobster. 2 p.

DFO. 1996g. Krill on the Scotian Shelf. DFO Atl. Fish. Stock Status Rep. 96/106E. 4 p.

DFO. 1996h. Coastal Zone Species Profile Series No. 2: Rock Crab. 2 p.

DFO. 1996i. Coastal Zone Species Profile Series No. 3: Toad Crab. 2 p.

DFO. 1996j. Coastal Zone Species Profile Series No. 4: Green Sea Urchin. 2 p.

DFO. 1997a. Whelk in the coastal waters of Québec. DFO Sci. Stock Status Rep. C4-09. 5 p.

DFO. 1997b. Southwest and eastern Nova Scotia blue mussels. DFO Atl. Fish. Stock Status Rep. 96/126E. 2 p.

DFO. 1997c. Iceland scallop: Grand Banks of Newfoundland (NAFO Div. 3LN) and Strait of Belle Isle (NAFO Div. 4R). DFO Sci. Stock Status Rep. C2-07. 6 p.

DFO. 1997d. Scotian Shelf Sea Cucumber. DFO Atl. Fish. Stock Status Rep. 96/125E. 2 p.

DFO. 1998a. Periwinkle (*Littorina littorea*). DFO Sci. Stock Status Rep. C3-46. 5 p.

DFO. 1998b. Scotian Shelf Ocean Quahaug. DFO Sci. Stock Status Rep. C3-37. 4 p.

DFO. 1998c. Browns Bank Scallop. DFO Sci. Stock Status Rep.C3-18. 5 p.

DFO. 1999. Banquereau Bank Arctic Surfclam. DFO Sci. Stock Status Rep. C3-34. 3 p.

DFO. 2000a. Northern shrimp (*Pandalus borealis*)- Div. 0B to 3K. DFO Sci. Stock Status Rep. C2-05. 15 p.

DFO. 2000b. State of phytoplankton, zooplankton and krill on the Scotian Shelf in 1998. DFO Sci. Stock Status Rep. G3-02. 6 p.

DFO. 2000c. Rock Crab-Eastern Nova Scotia. DFO Sci. Stock Status Rep. C3-05 (2000). 5 p.

DFO. 2001a. Iceland scallop in Newfoundland and Labrador. DFO Sci. Stock Status Rep. C2-07 (2001). 6 p.

DFO. 2001b. Commercial Fishery Landings Data, 1998-1999.

DFO. 2002. Southern Gulf of St. Lawrence rock crab (Lobster Fishing Areas 23, 24, 25, 26A and 26B). DFO Sci. Stock Status Rep. C3-04 (2002). 7 p.

DFO. 2003a. Newfoundland Lobster. DFO Sci. Stock Status Rep. 2003/022. 11 p.

DFO. 2003b. Northern Shrimp (*Pandalus borealis*)-Div. 0B to 3K. DFO Can. Sci. Advis. Sec. Stock Status Rep. 2003/036. 10 p.

DFO. 2003c. Newfoundland and Labrador Snow Crab. DFO Sci. Stock Status Rep. 2003/021. 15 p.

DFO. 2004a. The Stimpson's Surfclam in Quebec coastal waters in 2003. DFO Can. Stock. Assess. Sec., Stock Status Rep. 2004/002. 7 p.

DFO. 2004b. Eastern Nova Scotia Snow Crab. DFO Sci. Stock Status Rep. 2004/028. 15 p.

DFO. 2006a. Landings and Landed Value by Species, Newfoundland Region, 2004. November, 2006.

DFO. 2006b. Assessment of Division 0B – 3K Northern Shrimp. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2006/007. 19 p.

DFO. 2007a. Sea Scallop Status on St. Pierre Bank. DFO Can. Sci. Advis. Sec. Sci. Resp. 2007/006. 12 p.

DFO. 2007b. Assessment of Northern Shrimp on the Eastern Scotian Shelf (SFA 13-15). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/045. 12 p.

DFO. 2007c. Assessment of Snow Crab in the Western Gulf of St. Lawrence (Area 19). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/022. 11 p.

DFO. 2007d. Assessment of Southwestern Nova Scotia (4X) Snow Crab. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/040. 21 p.

DFO. 2007e. Landings and Landed Value by Species, Newfoundland Region, 2006.

DFO. 2007f. Assessment of Newfoundland and Labrador Snow Crab. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2007/008. 28 p.

DFO. 2007g. Rock Crab of the Coastal Waters of Quebec in 2006. DFO Can. Sci. Advis. Sec. Sci. advis. Rep. 2007/033. 12 p.

DFO. 2008a. Assessment of shrimp stocks in the Estuary and Gulf of St. Lawrence in 2007. DFO Can. Sci. Advis. Sec., Sci. Advis. Rep. 2008/002. 12 p.

DFO. 2008b. Assessment of northern shrimp (*Pandalus borealis*) and striped shrimp (*Pandalus montagui*) in shrimp fishing areas 0, 2 and 3. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2008/018. 19 p.

DFO. 2008c. Assessment of Nova Scotia (4VWX) Snow Crab. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2008/020. 22 p.

DFO. 2008d. Assessment of Newfoundland and Labrador Snow Crab. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2008/009. 42 p.

DFO. 2008e. Assessment of the rock crab (*Cancer irroratus*) fishery in the Southern Gulf of St. Lawrence Lobster Fishing Areas (LFA's) 23, 24, 25, 26A & 26B for 2000 to 2006. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2008/022. 9 p.

Dick, M.H., Donaldson, W.E. and Vining, I.W. 1998. Epibionts of the tanner crab *Chionoecetes bairdi* in the region of Kodiak Island, Alaska. J. Crust. Biol. 18(3): 519-528.

Dickie, L.M. 1955. Fluctuations in abundance of the giant sea scallops *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. J. Fish. Res. Board Can. 15: 1189-1211.

Dionne, M., Sainte-Marie, B., Bourget, E. and Gilbert, D. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. Mar. Ecol. Prog. Ser. 259: 117-128.

Dolgov, A.V. and Yaragina, N.A. 1990. Daily feeding rhythms and food intake of the Barents Sea cod and haddock in the summer of 1989. ICES CM 1990/G:6. 22 p.

Dooley, T. 1994. Developing a commercial sea urchin fishery in Newfoundland. Newfoundland and Labrador Department of Fisheries, Harvesting Operations Division. 10 p.

Drinkwater, K., Hannah, C., Loder, J., Harding, G. and Shore J. 2001. Modelling the drift of lobster larvae off southwest Nova Scotia. Can. Sci. Advis. Secret. Res. Doc. 2001/051.

Drouin, G., Himmelman, J.H. and Béland, P. 1985. Impact of tidal salinity fluctuations on echinoderm and mollusc populations. Can. J. Zool. 63: 1377-1387.

Duggan, R., Kenchington, E., Smith, S. and McLane, J.T. 1998. Preliminary stock survey of the ocean quahog (*Arctica islandica*) in St. Mary's Bay, Nova Scotia. DFO CSAS Res. Doc. 98/54. 18 p.

Dumas, J.V. and Witman, J.D. 1993. Predation by herring gulls (*Larus argentatus* Coues) and two rocky intertidal crab species [*Carcinus maenas* (L.) & *Cancer irroratus* Say]. J. Exp. Mar. Biol. Ecol. 169: 89-101.

Dumont, C., Himmelman, J.H. and Russell, M.P. 2004. Size-specific movement of green sea urchins *Strongylocentrotus droebachiensis* on urchin barrens in eastern Canada. Mar. Ecol. Prog. Ser. 276: 93-101.

Dunn, R., Mullineaux, L.S. and Mills, S. 1999. Resuspension of postlarval softshell clams *Mya arenaria* through disturbance by the mud snail *Ilyanassa obsoleta*. Mar. Ecol. Prog. Ser. 180: 223-232.

Eastman, N. 1995. Evaluating the possibility of a sea urchin industry in Newfoundland. Newfoundland and Labrador Department of Fisheries, Food and Agriculture. 44 p.

Ebert, T.A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. Ecology 49: 1075-1091.

Eckman, J. E. and Duggins, D.O. 1993. Effects of flow speed on growth of benthic suspension feeders. Biol. Bull. 185: 28-41.

Edwards, M. and Davies, M.S. 2002. Functional and ecological aspects of the mucus trails of the intertidal prosobranch gastropod *Littorina littorea*. Mar. Ecol. Prog. Ser. 238: 129-137.

Ellis, D.V. and Ronaldson, L.D. 1988. *Nephtys cornuta* (Polychaeta: Nephtydae) and its subspecies and use of the trinomials in pollution monitoring. Can. J. Zool. 66: 1898-1900.

Ellis, S.L. and Cowan, D.F. 2001. Volunteer-based monitoring of juvenile American lobster, *Homarus americanus*. Mar. Freshw. Res. 52(8): 1103-1112.

Elner, R.W. 1985. Crabs of the Atlantic coast of Canada. DFO Underwater World Factsheet UW/43: 8 p.

Elner, R.W. and Beninger, P.G. 1995. Multiple reproductive strategies in snow crab, *Chionoecetes opilio*: Physiological pathways and behavioral plasticity. J. Exp. Mar. Biol. Ecol. 193: 93-112.

Elner, R.W. and Campbell, A. 1987. Natural diets of lobster *Homarus americanus* from barren ground and macroalgal habitats off southwestern Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 37: 131-140.

Emerson, C.W. and Grant, J. 1991. The control of softshell clam (*Mya arenaria*) recruitment on intertidal sandflats by bedload sediment transport. Limnol. Oceanogr. 36(7): 1288-1300.

Emerson, I.P. 1973. Aspects of the biology and local distribution of sea-stars inhabiting a sloped, rocky bottom in Logy Bay, Newfoundland. M.Sc. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland. 302 p.

Ennis, G.P. 1973. Food, feeding and condition of lobsters, *Homarus americanus*, throughout the seasonal cycle in Bonavista Bay, Newfoundland. J. Fish. Res. Board Can. 30: 1905-1909.

Ennis, G.P. 1975. Observations on hatching and larval release in the lobster *Homarus americanus*. J. Fish. Res. Board Can. 31(11): 2210-2213.

Ennis, G.P. 1983a. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland near-shore area. Can. Tech. Rep. Fish. Aquat. Sci. 1138. 19 p.

Ennis, G.P. 1983b. Observations on the behaviour and activity of lobsters, *Homarus americanus*, in nature. Can. Tech. Rep. Fish. Aquat. Sci. 1165. 26 p.

Ennis, G.P. 1984. Small-scale seasonal movements of the American lobster *Homarus americanus*. Trans. Amer. Fish. Soc. 113: 336-338.

Ennis, G.P. 1995. Larval and postlarval ecology. p. 23-46. *In* J.R. Factor (ed.). Biology of the lobster *Homarus americanus*. Academic Press, San Diego, CA

Ennis, G.P., Collins, P.W., Badcock, G.D. and Dawe, G. 1997. Review of the Newfoundland lobster fishery. DFO CSAS Res. Doc. 97/126. 49 p.

Ennis, G.P., Hooper, R.G. and Taylor, D.M. 1990. Changes in the composition of snow crab (*Chionoecetes opilio*) participating in the annual breeding migration in Bonne Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 47: 2242-2249.

Erlandsson, J. 2002. Do reproductive strategy and breeding season influence the presence of mate recognition in the intertidal snail *Littorina*? Invert. Reprod. Develop. 41(1-3): 53-60.

Fader, G.B., King, L.H. and Josenhans, H.W. 1982. Surficial geology of the Laurentian Channel and the western Grand Banks of Newfoundland. Marine Sciences Paper 21. Geological Survey of Canada Paper 81-22.

Fahy, E., Masterson, E., Swords, D. and Forrest, N. 2000. A second assessment of the whelk fishery *Buccinum undatum* in the southwest Irish Sea with particular reference to its history of management by size limit. Marine Fisheries Services Division, Marine Institute, Abbotstown, Castleknock, Dublin 15. 67 p.

Falcon, L.I., Vecchione, M. and Roper, C.F.E. 2000. Paralarval gonatid squids (Cephalopoda: Oegopsida) from the Mid-North Atlantic Ocean. Proc. Biol. Soc. Washington 113(2): 532-541.

Falk, K. and Durinck, J. 1993. The winter diet of thick-billed murres, *Uria lomvia*, in western Greenland, 1988-1989. Can. J. Zool. 71: 264-272.

Falk-Petersen, I-B. 1982. Breeding season and egg morphology of echinoderms in Balsfjorden, northern Norway. Sarsia 67: 215-221.

Falkenhaug, T. 1996. Distributional and seasonal patterns of ctenophores in Malangen, northern Norway. Mar. Ecol. Prog. Ser. 140: 59-70.

Fay, C.W., Neves, R.J. and Pardue, G.B. 1983. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic) – Surfclam. FWS/OBS-82/11-13 TR EL-82-4. Fish Wildl. Serv., U.S. Dep. Int. and Coastal Ecology Group, Waterways Experiment Station, U.S. Army Corps Eng. 26 p.

FDP (Fisheries Diversification Program). 2002. Toad crab (*Hyas araneus*) surveys conducted. Emerging Fisheries Development Project Report FDP 358-1. 4 p.

Feindel, S.C. 2000. Optimization of hatchery culture of the sea scallop, *Placopecten magellanicus* (Bmelin, 1791): dietary lipid quality and fatty acid requirements. Thesis (M.Sc.), Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 215 p.

Feist, S.W., Bignell, J., Jones, G.J. and Stentiford, G.D. 2002. Measurements of histological changes in fish larvae, blue mussels and caged fish. ICES Biological Effects of Contaminants in Marine Pelagic Ecosystems CM 2002/X:11.

Figler, M.H., Peeke, H.V.S. and Chang, E.S. 1998. Shelter-related aggression between adult male conspecific intruders and resident maternal American lobsters (*Homarus americanus*) with eggs at different stages of embryogenesis. Mar. Freshw. Behav. Phy. 31: 151-166.

Fiorentino, J.F. and Witman, J.D. 1995. The foraging ecology of the waved whelk Buccinum undatum: The role of chemoreception in interactions with aggregating sea stars. Twenty-Third Benthic Ecology Meeting. Rutgers-the State University, New Brunswick, NJ, Inst. Marine Coastal Sciences.

Fisher, K.I. and Stewart, R.E.A. 1997. Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in northern Foxe Basin, Northwest Territories. Can. J. Zool. 75: 1166-1175.

Flach, E.C. 2003. The separate and combined effects of epibenthic predation and presence of macro-infauna on the recruitment success of bivalves in shallow soft-bottom areas on the Swedish west coast. J. Sea Res. 49(1): 59-67.

Flight, J. 1988. The 1987 whelk fishery in the Newfoundland region, 1987. Can. Tech. Rep. Fish. Aquat. Sci. 1630. 43 p.

Floyd, T. and Williams, J. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of softshell clams (*Mya arenaria* L.) in the southern Gulf of St. Lawrence. J. Shellfish Res. 23(2): 457-462.

Fogarty, M.J. 1981. Distribution and relative abundance of the ocean quahog *Arctica islandica* in Rhode Island Sound and off Martha's Vineyard, Massachusetts. J. Shellfish Res. 1: 33-39.

Folkow, L.P. and Blix, A.S. 1999. Diving behaviour of hooded seals (*Cystophora cristata*) in the Greenland and Norwegian Seas. Polar Biol. 22: 61-74.

Fossi, M.C., Borsani, J.F., Di Mento, R., Marsili, L., Casini, S., Neri, G., Mori, G., Ancora, S., Leonzio, C., Minutoli, R. and Notarbartolo di Sciara, G. 2002. Multi-trial biomarker approach in *Meganyctiphanes norvegica*: a potential early indicator of health status of the Mediterranean "whale sanctuary". Mar. Environ. Res. 54: 761-767.

Fournier, M., Pellerin, J., Lebeuf, M., Brousseau, P., Morin, Y. and Cyr, D. 2002. Effects of exposure of *Mya arenaria* and *Mactromeris polynyma* to contaminated marine sediments on phagocytic activity of haemocytes. Aquat. Toxicol. 59(1-2): 83-92.

Frank, K.T. 1986. Ecological significance of the ctenophore *Pleurobrachia pileus* off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 211-222.

Fraser, C.M. 1915. Pelagic hydroids. Bull. Mus. Comp. Zool. 59: 306-314.

Frechette, M. and Daigle, G. 2002a. Reduced growth of Iceland scallops *Chlamys islandica* (O.F. Muller) cultured near the bottom: A modeling study of alternative hypotheses. J. Shellfish Res. 21(1): 87-91.

Frechette, M. and Daigle, G. 2002b. Growth, survival and fluctuating asymmetry of Iceland scallops in a test of density-dependent growth in a natural bed. J. Exp. Mar. Biol. Ecol. 270(1): 73-91.

Freeman, K.R. 1974. Growth, mortality and seasonal cycle of *Mytilus edulis* in two Nova Scotian embayments. Fish. Mar. Serv. Tech. Rep. 500. 112 p.

Freeman, K.R. and Dickie, L.M. 1979. Growth and mortality of the blue mussel (*Mytilus edulis*) in relation to environmental indexing. J. Fish. Res. Board. Can. 36: 1238-1249.

Freeman, K.R., Perry, K.L. and DiBacco, T.G. 1992. Morphology, condition and reproduction of two co-occurring species of *Mytilus* at a Nova Scotia mussel farm. Bull. Aquacult. Assoc. Can. 92-3: 8-10.

Gagne, F., Blaise, C., Pellerin, J., Pelletier, E., Douville, M., Gauthier-Clerc, S. and Viglino, L. 2003. Sex alteration in softshell clams (*Mya arenaria*) in an intertidal zone of the Saint Lawrence River (Quebec, Canada). Comp. Biochem. Physiol., C: Toxicol. Pharmacol. 134(2): 189-198.

Gagnon, J-M. and K. Gilkinson. 1994. Discrimination and distribution of the sea urchins *Strongylocentrotus droebachiensis* (O.F. Müller) and *S. pallidus* (G.O. Sars) in the Northwest Atlantic. Sarsia 79: 1-11.

Gagnon, P., Himmelman, J.H. and Johnson, L.E. 2003a. Algal colonization in urchin barrens: defense by association during recruitment of the brown alga *Agarum cribrosum*. J. Exp. Mar. Biol. Ecol. 290: 179-196.

Gagnon, P., Himmelman, J.H. and Johnson, L.E. 2004. Temporal variation in community interfaces: kelp-bed boundary dynamics adjacent to persistent urchin barrens. Mar. Biol. 144: 1191-1203.

Gagnon, P., Johnson, L.E. and Himmelman, J.H. 2005. Kelp patch dynamics in the face of intense herbivory: stability of *Agarum clathratum* (Phaeophyta) stands and associated flora on urchin barrens. J. Phycol. 41: 498-505.

Gagnon, P., St-Hilaire-Gravel, L.V., Himmelman, J.H. and Johnson, L.E. 2006. Organismal defenses versus environmentally mediated protection from herbivores: Unraveling the puzzling case of *Desmarestia viridis* (Phaeophyta). J. Exp. Mar. Biol. Ecol. 334: 10-19.

Gagnon, P., Wagner, G. and Himmelman, J.H. 2003b. Use of a wave tank to study the effects of water motion and algal movement on the displacement of the sea star *Asterias vulgaris* towards its prey. Mar. Ecol. Prog. Ser. 258: 125-132.

Galand, P.E. and Fevolden, S.-E. 2000. Population structure of *Chlamys islandica* in the Northeast Atlantic-northern stocks compared with a southern relict population. Sarsia 85: 183-188.

Gallager, S.M., Davis, C.S., Epstein, A.W., Solow, A. and Beardsley, R.C. 1996. High-resolution observations of plankton spatial distributions correlated with hydrography in the Great South Channel, Georges Bank. Deep Sea Res. (II Top. Stud. Oceanogr.) 43(7-8): 1627-1663.

Galloway, T.S., Brown, R.J., Browne, M.A., Dissanayake, A., Lowe, D., Jones, M.B. and Depledge, M.H. 2004. A multibiomarker approach to environmental assessment. Environ. Sci. Tech. 38: 1723-1731.

Gannon, D.P., Read, A.J., Craddock, J.E., Fristrup, K.M. and Nicolas, J.R. 1997. Feeding ecology of long-finned pilot whales *Globicephala melas* in the western North Atlantic. Mar. Ecol. Prog. Ser. 148: 1-10.

Garcia, E.G., Thorarinsdottir, G.G. and Ragnarsson, S.A. 2003. Settlement of bivalve spat on artificial collectors in Eyjafjordur, North Iceland. Hydrobiologia 503: 131-141.

Gardner, G.A. and Howell, E.T. 1983. Zooplankton distribution across the shelf break on the Southeast Shoal of the Newfoundland Grand Banks in May 1981. Can. Manuscr. Rep. Fish. Aquat. Sci. 1724. 15 p.

Gardner, J.P. and Thomas, M.L.H. 1987. Growth and production of a *Littorina littorea* (L.) population in the Bay of Fundy. Ophelia 27(3): 181-195.

Gardner, J.P.A. and Thompson, R.J. 2001. The effects of coastal and estuarine conditions on the physiology and survivorship of the mussels *Mytilus edulis*, *M. trossulus* and their hybrids. J. Exp. Mar. Biol. Ecol. 265(2): 119-140.

Garrido, C.L. and Barber, B.J. 2001. Effects of temperature and food ration on gonad growth and oogenesis of the green sea urchin, *Strongylocentrotus droebachiensis*. Mar. Biol. 138: 447-456.

Garrison, L.P. 2000. Spatial and dietary overlap in the Georges Bank groundfish community. Can. J. Fish. Aquat. Sci. 57: 1679-1691.

Garthe, S., Montevecchi, W.A., Ojowski, U. and Stenhouse, I.J. 2004. Diets of northern fulmar (*Fulmarus glacialis*) chicks in the northwest Atlantic Ocean. Polar Biol. 27(5): 277-280.

Gauthier-Clerc, S., Pellerin, S., Blaise, J. and Gagne, F. 2002. Delayed gametogenesis of *Mya arenaria* in the Saguenay fjord (Canada): a consequence of endocrine disruptors? Comp. Biochem. Physiol. C: Toxicol. Pharmacol. 131(4): 457-467.

Gaymer, C.F. and Himmelman, J.H. 2002. Mussel beds in deeper water provide an unusual situation for competitive interactions between the sea stars *Leptasterias polaris* and *Asterias vulgaris*. J. Exp. Mar. Biol. Ecol. 277(1): 13-24.

Gaymer, C.F., Himmelman, J.H. and Johnson, L.E. 2001a. Distribution and feeding ecology of the seastars *Leptasterias polaris* and *Asterias vulgaris* in the northern Gulf of St. Lawrence, Canada. J. Mar. Biol. Assoc. U.K. 81: 827-843.

Gaymer, C.F., Himmelman, J.H. and Johnson, L.E. 2001b. Use of prey resources by the seastars *Leptasterias polaris* and *Asterias vulgaris*: a comparison between field observations and laboratory experiments. J. Exp. Mar. Biol. Ecol. 262(1): 13-30.

Gaymer, C.F., Himmelman, J.H. and Johnson, L.E. 2002. Effect of intra- and interspecific interactions on the feeding behavior of two subtidal sea stars. Mar. Ecol. Prog. Ser. 232: 149-162.

Gelsleichter, J., Musick, J.A. and Nichols, S. 1999. Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terranovae* and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. Environ. Biol. Fish. 54(2): 205-217

Gendron, L. 1992. Determination of the size at sexual maturity of the waved whelk *Buccinum undatum* Linnaeus, 1758, in the Gulf of St. Lawrence, as a basis for the establishment of a minimum catchable size. J. Shellfish Res. 11: 1-7.

Gendron, L., Fradette, P. and Godbout, G. 2001. The importance of rock crab (*Cancer irroratus*) for growth, condition and ovary development of adult American lobster (*Homarus americanus*). J. Exp. Mar. Biol. Ecol. 262(2): 221-241. vii, 20 p.

Gendron, L., Weise, A.M., Fréchette, M., Ouellet, P., McKindsey, C.W. and Girard, L. 2003. Evaluation of the potential of cultured mussels (*Mytilus edulis*) to ingest stage I lobster (*Homarus americanus*) larvae. Can. Ind. Rep. Fish. Aquat. Sci. 274.

Gendron, R.P. 1977. Habitat selection and migratory behaviour of the intertidal gastropod *Littorina littorea*. J. Anim. Ecol. 46: 79-92.

Ghiold, J. 1983. The role of external appendages in the distribution and life habits of the sand dollar *Echinarachnius parma* (Echinodermata: Echinoidea). J. Zool. 200: 405-419.

Gibeault, C.A. 1995. Habitat use by *Cancer borealis* and *C. irroratus* in the southern Gulf of Maine. Twenty-Third Benthic Ecology Meeting, New Brunswick, New Jersey, 17-19 March, 1995. Abstract.

Giguere, M., Cliche, G. and Brulotte, S. 1993. Reproduction of sea scallops (*Placopecten magellanicus*) and Iceland scallops (*Chlamys islandica*) in the Magdalen Islands. J. Shellfish Res. 12(1): 155.

Giguere, M., Cliche, G. and Brulotte, S. 1994. Reproductive cycles of the sea scallop, *Placopecten magellanicus* (Gmelin) and the Iceland scallop, *Chlamys islandica* (O.F. Müller), in Îles-de-la-Madeleine, Canada. J. Shellfish Res. 13(1): 31-36.

Gilbert, R., Aitken, A. and McLaughlin, B. 1984. A survey of coastal environments in the vicinity of Nain, Labrador. Atl. Geol. 20: 143-155.

Gilfillan, E.S. and Vallas, D.L. 1984. Observations of scope for growth, aspartate aminotransferase activity and glucose-6-phosphate dehydrogenase activity in *Mya truncata* and *Serripes groenlandicus* exposed to various concentrations of chemically dispersed crude oil in the DIAND/BIOS 1983 tank study. Working report series (Baffin Island Oil Spill Project, Canada). 83-7. 55 p.

Gilkinson, K. D. and Gagnon, J.-M. 1991. Substratum associations of natural populations of Iceland scallops, *Chlamys islandica* Müller 1776, on the northeastern Grand Bank of Newfoundland. Am. Malacol. Bull. 9(1): 59-67.

Gilkinson, K., Gagnon, J.-M., and Schneider, D.C. 1988. The sea urchin *Strongylocentrotus pallidus* (G.O. Sars) on the Grand Bank of Newfoundland. P. 467-473. *In* R.D. Burke, P.V. Mladenov, P. Lambert and R.L. Parsley (eds.) Echinoderm Biology. Proceedings of the Sixth International Echinoderm Conference, Victoria, B.C. 23-28 August, 1987.

Gilkinson, K. and Methven, D.A. 1991. Observations on the subtidal distributions of the intertidal Rough Periwinkle, *Littorina saxatilis*, and the common periwinkle, *L. littorea*, in a shallow embayment in eastern Newfoundland. Can. Field-Nat. 105: 522-525.

Gilkinson, K., Paulin, M., Hurley, S. and Schwinghamer, P. 1998. Impacts of trawl door scouring on infaunal bivalves: results of a physical trawl door model/dense sand interaction. J. Exp. Mar. Biol. Ecol. 224: 291-312.

Gillingham, J. and Penny, S. 1993. Newfoundland sea urchins: The new pearls of the sea. Report prepared for Canadian Centre for Fisheries Innovation. 43 p.

Giri, T. and Wicksten, M.K. 2002. Fouling of the caridean shrimp, *Lysmata wurdemanni* (Gibbes, 1850) by the barnacle, *Balanus inprovisus* Darwin, 1854 and other epibionts. Crustaceana 74(11): 1305-1314.

Gislason, A. and Astthorsson, O.S. 2000. The food of Norwegian spring spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. ICES CM 2000/M:9. 17 p.

Gislason, A. and Astthorsson, O.S. 2002. The food of Norwegian spring spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. Sarsia 87(3): 236-247.

Goldstein, J.S. and Tlusty, M.F. 2003. Substrate determinants and developmental rate of claw asymmetry in American lobsters, *Homarus americanus*. J. Crust. Biol. 23(4): 890-896.

Golikov, A.N. and Scarlato, O.A. 1973. Method for indirectly defining optimum temperatures of inhabitancy for marine cold-blooded animals. Mar. Biol. 20: 1-5.

Gonor, J.J. 1973. Reproductive cycles in Oregon populations of the echinoid, *Strongylocentrotus purpuratus* (Stimpson). I. Annual gonad growth and ovarian gametogenic cycles. J. Exp. Mar. Biol. Ecol. 12: 45-64.

Gordon, D.C., Jr., Cranford, P.J., Hannah, C.G., Loder, J.W., Milligan, T.G., Muschenheim, D.K. and Shen, Y. 2001. Modelling the transport and effects on scallops of water-based drilling mud from potential hydrocarbon exploration on Georges Bank. Can. Tech. Rep. Fish. Aquat. Sci. 2317. 166 p.

Gosner, K.L. 1979. A field guide to the Atlantic seashore from the Bay of Fundy to Cape Hatteras. The Peterson Field Guide Series. 329 p.

Government of Canada. 2010. Speceis Profile: Leatherback Sea Turtle. Species at Risk Public Registry. http://www.sararegistry.gc.ca/species/speciesDetails_e.cfm?sid=274.

Government of Newfoundland and Labrador. 2002. Jellyfish Exploratory Survey, Trinity Bay. Department of Fisheries and Aquaculture, Fisheries Diversification Program. Project Summary: FDP 424 – 5. 4 p.

Government of Newfoundland and Labrador. 2005. Seafood Industry 2005 Year in Review. Newfoundland and Labrador Department of Fisheries and Aquaculture. St. John's, NL. 20 p.

Grabe, S.A. 2003. Seasonal periodicity of decapod larvae and population dynamics of selected taxa in New Hampshire (U.S.A.) coastal waters. J. Plankton Res. 25(4): 417-428.

Graham, W.M. and Kroutil, R.M. 2001. Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. J. Plankton Res. 23(1): 67-74.

Granéli, E. and Turner, J.T. 2002. Top-down regulation in ctenophore-copepod-ciliate-diatom-phytoflagellate communities in coastal waters: a mesocosm study. Mar. Ecol. Prog. Ser. 239: 57-68.

Grant, J. and Thorpe, B. 1991. Effects of suspended sediment on growth, respiration and excretion of the softshell clam (*Mya arenaria*). Can. J. Fish. Aquat. Sci. 48: 1285-1292.

Grant, W.C. 1963. Notes of the ecology and behaviour of the hermit crab, *Pagurus acadianus*. Ecology 44: 767-771.

Grassle, J.F., Sanders, H.L., Hessler, R.R., Rowe, G.T. and McLellan, T. 1975. Pattern and zonation: a study of the bathyal megafauna using the research submersible Alvin. Deep-Sea Res. 22: 457-481.

Green, G.A. and Brueggeman, J.J. 1991. Sea otter diets in a declining population in Alaska. Mar. Mam. Sci. 7(4): 395-401.

Greenway, S.C. and Storey, K.B. 2001. Effects of seasonal change and prolonged anoxia on metabolic enzymes of *Littorina littorea*. Can. J. Zool. 79: 907-915.

Greve, W. 1973. Ecological investigations on *Pleurobrachia pileus*. 2. Laboratory investigations. Fish. Res. Board Can. Trans. Ser. 2672. 36 p.

Griswold, C.A. and Prezioso, J. 1981. In situ observations on reproductive behaviour of the long-finned squid, *Loligo pealeii*. Fish. Bull. 78(4): 945-947.

Gudimova, E.N. 1998. Prospects of sea cucumber fishing in the Barents Sea. Rybn. Khoz. (Mosc.) 3: 45-46.

Guillemette, M., Ydenberg, R.C. and Himmelman, J.H. 1992. The role of energy intake in prey and habitat selection of common eiders *Somateria mollissima* in winter: a risk-sensitive interpretation. J. Anim. Ecol. 61: 599-610.

Haakonsen, H.O. and Anoruo, A.O. 1994. Tagging and migration of the American lobster *Homarus americanus*. Rev. Fish. Sci. 2(1): 79-93.

Hagen, N.T. Anderson, A. and Stabell, O.B. 2002. Alarm responses of the green sea urchin, *Strongylocentrotus droebachiensis*, induced by chemically labeled durophagous predators and simulated acts of predation. Mar. Biol. 140(2): 365-374.

Hamel, J-F. and Himmelman, J.H. 1992. Sexual dimorphism in the sand dollar *Echinarachnius parma*. Mar. Biol. 113: 379-383.

Hamel, J-F and Mercier, A. 1995. Prespawning behaviour, spawning and development of the brooding starfish *Leptasterias polaris*. Biol. Bull. 188: 32-45.

Hamel, J.-F. and Mercier, A. 1996a. Evidence of chemical communication during the gametogenesis of holothuroids. Ecology 77(5): 1600-1616.

Hamel, J.-F. and Mercier, A. 1996b. Early development, settlement, growth and spatial distribution of the sea cucumber *Cucumaria frondosa* (Echinodermata: Holothuroidea). Can. J. Fish. Aquat. Sci. 53: 253-271.

Hamel, J.-F. and Mercier, A. 1998. Diet and feeding behaviour of the sea cucumber *Cucumaria frondosa* in the St. Lawrence estuary, eastern Canada. Can. J. Zool. 76: 1194-1198.

Hamer, J.P. and Walker, G. 2001. Avoidance of dried biofilms on slate and algal surfaces by certain spirorbid and bryozoan larvae. J. Mar. Biol. Assoc. U.K. 81(1): 167-168.

Hamoutene, D., Payne, J.F., French, B., Veinott, G. and Fancey, L. 2002. Effect of copper mine tailings on lipid peroxidation, DNA damage and histopathology in softshell clams (*Mya arenaria*) at Little Bay, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 2436. iv + 12 p.

Hanson, J.M. and Lanteigne, M. 1999. Results of an experimental shrimp fishery in Chaleur Bay, southern Gulf of St. Lawrence. N. Am. J. Fish. Manage. 19: 713-723.

Hanson, J.M. and Lanteigne, M. 2000. Evaluation of Atlantic cod predation on American lobster in the southern Gulf of St. Lawrence, with comments on other potential fish predators. Trans. Am. Fish. Soc. 129: 13-29.

Hansson, L.J. 1997. Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea capillata* and prey response to predator contact. J. Plankton Res. 19(2): 195-208.

Harding, G.C.H. 1996. Ecological factors to be considered in establishing a new krill fishery in the Maritime Region. DFO Atl. Fish. Res. Doc. 96/99. 11 p.

Harding, G.C., Pringle, J.D., Vass, W.P., Pearre, S. and Smith, S. 1987. Vertical distribution and daily movements of larval *Homarus americanus* over Browns Bank, Nova Scotia. Mar. Ecol. Prog. Ser. 41: 29-41.

Harding, J.M. 2003. Evaluation of the neutral red assay as a stress indicator in mussels (*Mytilus* spp.) in relation to seasonal, environmental, handling, harvesting, processing and post-harvest storage conditions. Thesis (M.Sc.), Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 94 p.

Harms, J. and Seeger, B. 1989. Larval development and survival in seven decapod species (Crustacea) in relation to laboratory diet. J. Exp. Mar. Biol. Ecol. 133: 129-139.

Hart, M.W. 1991. Particle captures and the method of suspension feeding by echinoderm larvae. Biol. Bull. 180: 12-27.

Hartnoll, R.G. and Bryant, A.D. 2001. Growth to maturity of juveniles of the spider crabs *Hyas coarctatus* and *Inachus dorsettensis* (Pennant Brachyura: Majidae). J. Exp. Mar. Biol. Ecol. 263(2): 143-158.

Hartnoll, R.G., Bryant, A.D. and Gould, P. 1993. Size distribution in spider crab populations-spatial and temporal variation. J. Crust. Biol. 13(4): 647-655.

Harvell, C.D., Caswell, H. and Simpson, P. 1990. Density effects in a colonial monoculture: experimental studies with a marine bryozoan (*Membranipora membranacea* L.). Oecologia 82: 227-237.

Harvey, M., Bourget, E., Legault, C. and Ingram, R.G. 1995. Short-term variations in settlement and early spat mortality of Iceland scallop, *Chlamys islandica* (O.F. Müller). J. Exp. Mar. Biol. Ecol. 194: 167-187.

Harvey, M., Bourget, E. and Miron, G. 1993. Settlement of Iceland scallop *Chlamys islandica* spat in response to hydroids and filamentous red algae: field observations and laboratory experiments. Mar. Ecol. Prog. Ser. 99: 283-292.

Harvey, M. and Morrier, G. 2003. Laboratory feeding experiments on zoea of northern shrimp *Pandalus borealis* fed with natural zooplankton. Mar. Ecol. Prog. Ser. 265: 165-174.

Hatcher, B.G., Scheibling, R.E., Barbeau, M.A., Hennigar, A.W., Taylor, L.H. and Windust, A.J. 1996. Dispersion and mortality of a population of sea scallop (*Placopecten magellanicus*) seeded in a tidal channel. Can. J. Fish. Aquat. Sci. 53: 38-54.

Haug, T., Kjuul, A.K., Styrvold, O.B., Sandadalen, E., Olsen, Ø.M. and Stensvåg, K. 2002b. Antibacterial activity in *Strongylocentrotus droebachiensis* (Echinoidea), *Cucumaria frondosa* (Holothuroidea) and *Asterias rubens* (Asteroidea). J. Invertebr. Pathol. 81: 94-102.

Haug, T., Nilssen, K.T. and Lindblom, L. 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. Polar Res. 23(1): 35-42.

Haug, T., Lindstrom, U. and Nilssen, K.T. 2002a. Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. Sarsia 87(6): 409-422.

Hawkins, C.M. 1996. Environmental habitat quality requirements/guidelines for *Placopecten magellanicus*, Giant or Deep Sea Scallop. Report by Triton Consultants, Dartmouth, NS for Department of Fisheries and Oceans, Halifax, NS. 16 p.

Hawkins, C.M. 2000. Environmental habitat quality requirements/guidelines for green sea urchin, *Strongylocentrotus droebachiensis*. Report prepared by Triton Consultants for Habitat Planning, Fisheries and Oceans, Maritimes Region, Halifax, NS. 16 p.

Hayes, F.R. 1929. Contributions to the study of marine gastropods. Development, growth and behaviour of *Littorina*. Contrib. to Can. Bio. Fish. IV: 415-430.

Heilskov, A.C. and Holmer, M. 2003. Influence of benthic fauna on organic matter decomposition in organic-enriched fish farm sediments. Vie Milieu 53(4): 153-161.

Hendler, G. 1991. Echinodermata: Ophiuroidea. p. 355 – 511. *In* Giese, A.C., Pearse, J.S. and Pearse, V.B. (eds.). Reproduction of Marine Invertebrates, Volume VI: Echinoderms and Lophophorates. Boxwood Press, Pacific Grove, CA.

Hendrickson, L.C. 1999. Fishery effects on spawner escapement in the northwest Atlantic *Illex illecebrosus* stock. Sci. Counc. Res. Doc. NAFO 99/66. 8 p.

Hendrickson, L.C. 2004. Population biology of northern shortfin squid (*Illex illecebrosus*) in the Northwest Atlantic Ocean and initial documentation of a spawning area. ICES J. Mar. Sci. 61: 252-266.

Hendrickson, L.C., Dawe, E.G. and Showell, M.A. 2004. Assessment of northern shortfin squid (*Illex illecebrosus*) in Subareas 3+4 for 2003. Sci. Counc. Res. Doc. 04/38.

Henry, L.-A. 2002. Intertidal zonation and seasonality of the marine hydroid *Dynamena pumila* (Cnidaria: Hydrozoa). Can. J. Zool. 80: 1526-1536.

Henry, L.-A. and Kenchington, E. 2004. Differences between epilithic and epizoic hydroid assemblages from commercial scallop grounds in the Bay of Fundy, northwest Atlantic. Mar. Ecol. Prog. Ser. 266: 123-134.

Herman, A.W., Cochrane, N.A. and Sameoto, D.D. 1993. Detection and abundance estimation of euphausiids using an optical plankton counter. Mar. Ecol. Prog. Ser. 94: 165-173.

Herman, P.M.J., Middelburg, J.J. and Heip, C.H.R. 2001. Benthic community structure and sediment processes on an intertidal flat: results from the ECOFLAT project. Cont. Shelf Res. 21: 2055-2071.

Herra, T. 1988. Ichthyoplankton survey in the southern Baltic in August 1987. ICES CM 1988/L:23. Biological Oceanography Committee. 17 p.

Hiddink, J.G., ter Hofstede, R. and Wolff, W.J. 2002. Predation of intertidal infauna on juveniles of the bivalve *Macoma balthica*. J. Sea Res. 47(2): 141-159.

Highsmith, R.C. and Emlet, R.B. 1986. Delayed metamorphosis: effect on growth and survival of juvenile sand dollars (Echinoidea: Clypeasteroida). Bull. Mar. Sci. 39(2): 347-361.

Himmelman, J.H. 1977. Reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*. Can. J. Zool. 56: 1828-1836.

Himmelman, J.H. 1984. Urchin feeding and macroalgal distribution in Newfoundland, Eastern Canada. Can. Field-Nat. 111: 337-348.

Himmelman, J.H. 1988. Movements of whelks (*Buccinum undatum*) towards a baited trap. Mar. Biol. 97: 521-531.

Himmelman, J.H. 1991. Diving observations of subtidal communities in the northern Gulf of St. Lawrence, p. 319-332. *In* J.-C. Therriault (ed.). The Gulf of St. Lawrence: small ocean or big estuary? Can. Spec. Publ. Fish. Aquat. Sci. 113.

Himmelman, J.H., Cardinal, A. and Bourget, E. 1983. Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, Eastern Canada. Oecologia 59: 27-39.

Himmelman, J.H. and Dutil, C. 1991. Distribution, population structure and feeding of subtidal seastars in the northern Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 76: 61-72.

Himmelman, J.H., Guderley, H., Vignault, G., Drouin, G and Wells, P.G. 1984. Response of the sea urchin, *Strongylocentrotus droebachiensis*, to reduced salinities: importance of size, acclimation and interpopulation differences. Can. J. Zool. 62: 1015-1021.

Himmelman, J.H. and Hamel, J.R. 1993. Diet, behaviour and reproduction of the whelk *Buccinum undatum* in the northern Gulf of St. Lawrence, eastern Canada. Mar. Biol. 116: 423-430.

Himmelman, J.H., Lavergne, Y., Cardinal, A., Martel, G. and Jalbert, P. 1982. Brooding behaviour of the northern sea star *Leptasterias polaris*. Mar. Biol. 68: 235-240.

Himmelman, J.H. and Steele, D.H. 1971. Food and predators of the green sea urchin, *Strongylocentrotus droebachiensis*, in Newfoundland waters. Mar. Biol. 9: 315-322.

Hinz, H., Kröncke, I. and Ehrich, S. 2004. Seasonal and annual variability in an epifaunal community in the German Bight. Mar. Biol. 144: 735-745.

Hiscock, K., Southward, A., Tittley, I. and Hawkins, S. 2004. Effects of changing temperature on benthic marine life in Britain and Ireland. Aquat. Conserv.: Mar. Freshw. Ecosyst.. 14: 333-362.

Hjelset, A.M., Andersen, M., Gjertz, I., Lydersen, C. and Gulliksen, B. 1999. Feeding habits of beared seals (*Erignathus barbatus*) from the Svalbard area, Norway. Polar Biol. 21: 186-193.

Hollingshead, K.W. and Corey, S. 1974. Aspects of the life history of *Meganyctiphanes norvegica* (M. Sars), Crustacea (Euphausiacea), in Passamaquoddy Bay. Can. J. Zool. 52: 495-505.

Hooker, S.K., Iverson, S.J., Ostrom, P. and Smith, S.C. 2001. Diet of northern bottlenose whales inferred from fatty-acid and stable-isotope analyses of biopsy samples. Can. J. Zool. 79(8): 1442-1454.

Hooper, R.G. 1986. A spring breeding migration of the snow crab, *Chionoecetes opilio* (O. Fabr.), into shallow water in Newfoundland. Crustaceana 50(3): 257-264.

Hooper, R.G. 1997. A general coastal marine habitat classification system for Newfoundland. Draft report for Department of Fisheries and Oceans, Habitat Management, St. John's, Newfoundland. 14 p.

Hooper, R.G. and Cuthbert, F.M. 1993. A survey of southern Labrador sea urchins. Report for Comprehensive Labrador Cooperation Agreement, Happy Valley-Goose Bay, Labrador. 49 p.

Hooper, R.G., Cuthbert, F.M. and McKeever, T. 1996. Sea urchin aquaculture-Phase II: Ration size, seasonal growth rates, mixed kelp diets, fish diet, old urchin growth and baiting confinement experiments. Report for Canadian Centre for Fisheries Innovation. 34 p.

Hovde, S.C., Albert, O.T. and Nilssen, E.M. 2002. Spatial, seasonal and ontogenetic variation in diet of Northeast Arctic Greenland halibut (*Reinhardtius hippoglossoides*). ICES J. Mar. Sci. 59(2): 421-437.

Hudon, C. 1987. Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Îles de la Madeleine (Quebec). Can. J. Fish. Aquat. Sci. 44(11): 1855-1869.

Hudon, C. and Fradette, P. 1993. Wind-induced advection of larval decapods into Baie de Plaisance (Iles de la Madeleine, Québec). Can. J. Fish. Aquat. Sci. 50: 1422-1434.

Hudon, C., Fradette, P. and Legendre, P. 1986. La réparition horizontale et verticale des larves de homard (*Homarus americanus*) autour des îles de la Madelaine, golfe du Saint-Laurent. Can. J. Fish. Aquat. Sci. 43: 2164-2176.

Hudon, C. and Lamarche, G. 1989. Niche segregation between American lobster *Homarus americanus* and rock crab *Cancer irroratus*. Mar. Ecol. Prog. Ser. 52: 155-168.

Hughes, J.T. and Matthiessen, G.C. 1962. Observations on the biology of the American lobster, *Homarus americanus*. Limnol. Oceangr. 7: 1110-1111.

Hughes, S.E. and Bourne, N. 1981. Stock assessment and life history of a newly discovered Alaska surfclam (*Spisula polynyma*) resource in the southeastern Bering Sea. Can. J. Fish. Aquat. Sci. 38(10): 1173-1181.

Humes, A.G. and Voight, J.R. 1997. *Cholidya polypi* (Copepoda: Harpacticoida: Tisbidae), a parasite of deep-sea octopuses in the North Atlantic and Northeastern Pacific. Ophelia 46(1): 65-81.

Humphrey, B., Boehm, P.D., Hamilton, M.C. and Norstrom, R.J. 1987. The fate of chemically dispersed and untreated crude oil in Arctic benthic biota. Arctic 40 (suppl.1): 149-161.

Hunter, J. 1981. Feeding preferences and competitive herbivory studies on two species of periwinkles, *Littorina obtusata* and *Littorina littorea*. Biol. Bull. Mar. Biol. Lab. (Woods Hole) 161: 328.

Hurd, C.L., Durante, K.M., Chia, F.S., Harrison, P.J., 1994. Effect of bryozoan colonization on inorganic nitrogen acquisition by the kelps Agarum fimbriatum and *Macrocystis integrifolia*. Mar. Biol. 121: 167-173.

Hurd, C.L., Durante, K.M. and Harrison, P.J. 2000. Influence of bryozoan colonization on the physiology of the kelp *Macrocystis integrifolia* (Laminariales, Phaeophyta) from nitrogen-rich and –poor sites in Barkley Sound, British Columbia, Canada. Phycologia 39(5): 435-440.

Hurlbut, C.J. 1991. Larval substratum selection and postsettlement mortality as determinants of the distribution of two bryozoans. J. Exp. Mar. Biol. Ecol. 147: 103-119.

Incze, L.S. and Naimie, C.E. 2000. Modeling the transport of lobster (*Homarus americanus*) larvae and postlarvae in the Gulf of Maine. Fish. Oceanogr. 9: 99-113.

Incze, L.S., Wahle, R.A. and A.T. Palma. 2000. Advection and settlement rates in a benthic invertebrate: recruitment to first benthic stage in *Homarus americanus*. ICES J. Mar. Sci. 57: 430-437.

Iyengar, E.V. and Harvell, C.D. 2002. Specificity of cues inducing defensive spines in the bryozoan *Membranipora membranacea*. Mar. Ecol. Prog. Ser. 225: 205-218.

Jacobsen, H.P. and Stabell, O.B. 1999. Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light conditions and chemical labeling of predators. Mar. Biol. 134: 551-557.

Jalbert, P. and Himmelman, J.H. 1989. Whelks (*Buccinum undatum*) and other subtidal invertebrate predators in the northern Gulf of St. Lawrence. Nat. Can. 116(1): 1-15.

Jalbert, P., Himmelman, J.H., Beland, J.H. and Thomas, B. 1989. Whelks (*Buccinum undatum*) and other subtidal invertebrate predators in the northern Gulf of St. Lawrence. Nat. Can. 116: 1-15.

James-Pirri, M.-J. and Cobb, J.S. 2000. Influence of size and delayed settlement on the recapture rate of newly settled American lobsters *Homarus americanus*. Mar. Ecol. Prog. Ser. 208: 197-203.

James-Pirri, M.-J., Cobb, J.S. and Wahle, R.A. 1998. Influence of settlement time and size on postsettlement growth in the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 55: 2436-2446.

Jamieson, G.S., Stone, H. and Etter, M. 1982. Predation of sea scallops (*Placopecten magellanicus*) by lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in underwater cage enclosures. Can. J. Fish. Aquat. Sci. 39: 499-505.

Janke, K. 1986. Macrofauna and its distribution in the northeastern rocky intertidal zone of the island of Helgoland. Helgoländer Meeresun. 40: 1-55.

Jennings, J.B. and Hanna, F.S. 1988. Studies on the respiratory pigments of three species of serpulid polychaetes at different stages in the life cycle. Ophelia 29(3): 199-212.

Jewett, S.C., Feder, H.M. and Blanchard, A. 1999. Assessment of the benthic environment following offshore placer gold mining in the northeastern Bering Sea. Mar. Environ. Res. 48: 91-122.

Johannesson, K. and Ekendahl, A. 2002. Selective predation favouring cryptic individuals of marine snails (*Littorina*). Biol. J. Linn. Soc. 76(1): 137-144.

Jones, D.S. 1980. Reproductive cycles of the ocean quahog *Arctica islandica* and the Atlantic surfclam *Spisula solidissima*. Abstracts: 1980 Annual Meeting, June 9-12, National Shellfisheries Association, Hyannis, Massachusetts. p. 117.

Jones, D.S. 1981. Reproductive cycles of the Atlantic surfclam *Spisula solidissima* and the ocean quahog *Arctica islandica* off New Jersey. J. Shellfish Res. 1(1): 23-32.

Jones, L.T. 1969. Continuous plankton records: studies on the zooplankton east of Newfoundland and Labrador, with particular reference to the euphausiid *Thysanoessa longicaudata* (Krøyer). Bull. Mar. Ecol. 6: 275-300.

Jones, M.B. and Smaldon, G. 1989. Aspects of the biology of the cosmopolitan brittlestar *Amphipholis squamata* (Echinodermata) from the Firth of Forth, Scotland. J. Nat. Hist. 23: 613-625.

Jonsson, L.G., Lundälv, T. and Johannesson, K. 2001. Symbiotic associations between anthozoans and crustaceans in a temperate coastal area. Mar. Ecol. Prog. Ser. 209: 189-195.

Jørgensen, L.L., Pearson, T.H., Anisimova, N.A., Gulliksen, B., Dahle, S., Denisenko, S.G. and Matishov, G.G. 1999. Environmental influences on benthic fauna associations of the Kara Sea (Arctic Russia). Polar Biol. 22: 395-416.

Juanes, F., Buckel, J.A. and Scharf, F.S. 2001. Predatory behaviour and selectivity of a primary piscivore: comparison of fish and non-fish prey. Mar. Ecol. Prog. Ser. 217: 157-165.

Jury, S., Kinnison, Howell, M.T., and Watson, W.H., III, 1994. The behaviour of lobsters in response to reduced salinity. J. Exp. Mar. Biol. Ecol. 180: 23-37.

Jury, S.H. and Watson, W.H., III. 2000. Thermosensitivity of the lobster, *Homarus americanus*, as determined by cardiac assay. Biol. Bull. 199: 257-264.

Kaartvedt, S., Larsen, T., Hjelmseth, K. and Onsrud, M.S.R. 2002. Is the omnivorous krill *Meganyctiphanes norvegica* primarily a selectively feeding carnivore? Mar. Ecol. Prog. Ser. 228: 193-204.

Kaartvedt, S., Skjoldal, H.R., Melle, W. and Knutsen, T. 1993. Underwater optics and behavioral responses of krill to presence of fish predators affect fish-plankton interactions. ICES CM 1993/L:43. Biological Oceanography Committee. 14 p.

Karnofsky, E.B. and Price, H.J. 1989. Dominance, territoriality and mating in the lobster, *Homarus americanus*: a mesocosm study. Mar. Freshw. Behav. Phy. 15: 101-121.

Keats, D.W. 1990. Food of the winter flounder *Pseudopleuronectes americanus* in a sea urchin dominated community in eastern Newfoundland. Mar. Ecol. Prog. Ser. 60: 13-22.

Keats, D.W. 1991. American plaice, *Hippoglossoides platessoides* (Fabricius), predation on green sea urchins, *Strongylocentrotus droebachiensis* (O.F. Muller), in eastern Newfoundland. J. Fish. Biol. 38: 67-72.

Keats, D.W., Hooper, R.G., Steele, D.H. and South, G.R. 1987. Field observations of summer and autumn spawning by *Strongylocentrotus droebachiensis*, green sea urchins, in eastern Newfoundland. Can. Field-Nat. 101: 463-465.

Keats, D.W., Steele, D.H. and South, G.R. 1986a. Atlantic wolffish (*Anarhichas lupus* L.; Pisces: Anarhicidae) predation on green sea urchins (*Strongylocentrotus droebachiensis* (O.F. Mull.); Echinodermata: Echinoidea) in eastern Newfoundland. Can. J. Zool. 64: 1920-1925.

Keats, D.W., Steele, D.H. and South, G.R. 1986b. Ocean pout (*Macrozoarces americanus*) (Bloch and Schneider) (Pices: Zoarcidae) predation on green sea urchin (*Strongylocentrotus droebachiensis*) (O.F. Muller) (Echinodermata: Echinoidea) in eastern Newfoundland. Can. J. Zool. 65: 1515-1521.

Kenchington, E., Duggan, R. and Riddell, T. 1998. Early life history characteristics of the razor clam (*Ensis directus*) and the moonsnails (*Euspira* spp.) with applications to fisheries and aquaculture. Can. Tech. Rep. Fish. Aquat. Sci. 2223. 32 p.

Kenchington, E. and Glass, A. 1998. Local adaptation and sexual dimorphism in the waved whelk (*Buccinum undatum*) in Atlantic Nova Scotia with applications to fisheries management. Can. Tech. Rep. Fish. Aquat. Sci. 2237. 43 p.

Kenchington, E. and Lundy, M.J. 1996. A summary of a whelk (*Buccinum undatum*) test fishery in the Tusket Island area of southwest Nova Scotia with a review of biological characteristics relevant to the development of this resource. DFO Atl. Fish. Res. Doc. 96/12. 17 p.

Kenchington, E.L.R., Prena, J., Gilkinson, K.D., Gordon, D.C., Jr., MacIssac, K., Bourbonnais, C., Schwinghamer, P.J., Rowell, T.W., McKeown, D.L. and Vass, W.P. 2001. Effects of experimental otter trawling on the macrofauna of a sandy bottom ecosystem on the Grand Banks of Newfoundland. Can. J. Fish. Aquat. Sci. 58: 1043-1057.

Kenchington, E., Têtu, C. and Mohn, R. 1991. Preliminary investigations of juvenile scallops (*Placopecten magellanicus*) in Nova Scotia inshore habitats. Can. Manuscr. Rep. Fish. Aquat. Sci. 2123. 32 p.

Kennish, M.J., Lutz, R.A., Dobarro, J.A. and Fritz, L.W. 1994. *In situ* growth rates of the ocean quahog, *Arctica islandica* (Linnaeus, 1767), in the Middle Atlantic Bight. J. Shellfish Res. 13(2): 473-478.

Kerswill, C.J. 1949. Effects of water circulation on the growth of quahogs and oysters. J. Fish. Res. Board Can. 7(9): 545-551.

Key, M.M., Winston, J.E., Volpe, J.W., Jeffries, W.B. and Voris, H.K. 1999. Bryozoan fouling of the blue crab *Callinectes sapidus* at Beaufort, North Carolina. Bull. Mar. Sci. 64(3): 513-533.

Kideys, A.E, Nash, R.D.M. and Hartnoll, R.G. 1993. Reproductive cycle and energetic cost of reproduction of the neogastropod *Buccinum undatum* in the Irish Sea. J. Mar. Biol. Assoc. U.K. 73: 391–403.

Kideys, A.E. and Romanova, Z. 2001. Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996-1999. Mar. Biol. 139: 535-547.

King, A.J., Adamo, S.A. and Hanlon, R.T. 1999. Contact with squid egg capsules increases agonistic behavior in male squid (*Loligo pealeii*). Biol. Bull. 197(2): 256.

King, A.J., Adamo, S.A. and Hanlon, R.T. 2003. Squid egg mops provide sensory cues for increased agonistic behaviour between male squid. Anim. Behav. 66: 49-58.

Klages, M., Muyakshin, S., Soltwedel, T. and Arntz, W.E. 2002. Mechanoreception, a possible mechanism for food fall detection in deep-sea scavengers. Deep Sea Res. (I Oceanogr. Res. Pap.) 49(1): 143-155.

Klein-MacPhee, G., Sullivan, B.K., Van Keuren, D., Horgan, E. and Klos, E. 1997. Mortality of larval cod related to predation by the hydroid *Clytia gracilis*. ICES CM 1997//T:03. 7 p.

Koehl, M.A.R. 1999. Ecological biomechanics of benthic organisms: Life history, mechanical design and temporal patterns of mechanical stress. J. Exp. Biol. 202: 3469-3476.

Koeller, P. 1996. Aspects of the biology of northern shrimp *Pandalus borealis* on the Scotian Shelf. DFO Atl. Fish. Res. Doc. 96/9. 34 p.

Koeller, P., Covey, M. and King, M. 1996. The Scotian Shelf shrimp (*Pandalus borealis*) fishery in 1996. DFO Atl. Fish. Res. Doc. 96/128.

Kraft, J.C. and Gordon, E.B. 2001. Variations in the green sea urchin, *Strongylocentrotus drobachiensis*, by changing current to determine optimal conditions for future aquaculture purposes. Tech 797, Ocean projects. Sea Grant, New Hampshire. 28 p.

Kraus, M.G., Beal, B.F. and Chapman, S.R. 1990. Growth rate of *Arctica islandica* Linne: A comparison of wild and laboratory-reared individuals. Abstracts: 1990 Annual Meeting, April 1-5, National Shellfisheries Association, Williamsburg, Virginia. 463 p.

Kraus, M.G., Beal, B.F., Chapman, S.R. and McMartin, L. 1992. A comparison of growth rates in *Arctica islandica* (Linnaeus, 1767) between field and laboratory populations. J. Shellfish Res. 11(2): 289-294.

Kraus, M.G., Beal, B.F. and McMartin, L. 1991. Salinity and temperature tolerance tests on ocean quahogs, *Arctica islandica* (L.). Abstracts: 1991 Annual Meeting, June 23-27, National Shellfisheries Association, Williamsburg, Virginia. 297 p.

Kristensen, T.K. 1983. *Gonatus fabricii*. p. 159-173. *In* Boyle, P.R. (ed.). Cephalopod Life Cycles, Volume I, Species Accounts. Academic Press. London.

Kristensen, T.K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from west Greenland waters. Meddelelser om Grønland, Bioscience 13: 3-17.

Kristensen, E. and Mikkelsen, O.L. 2003. Impact of the burrow-dwelling polychaetes *Nereis diversicolor* on the degradation of fresh and aged macroalgal detritus in a coastal marine sediment. Mar. Ecol. Prog. Ser. 265: 141-153.

Kukliński, P. and Porter, J.S. 2004. *Alcyonidium disciforme*: an exceptional Arctic bryozoan. J. Mar. Biol. Assoc. U.K. 84: 267-275.

Kulka, D.W. and Corey, S. 1978. The life history of *Thysanoessa intermis* (Krøyer) in the Bay of Fundy. Can. J. Zool. 56: 492-506.

Kulka, D.W., Corey, S. and Iles, T.D. 1982. Community structure and biomass of euphausiids in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 39: 326-334.

Kupriyanova, E.K., Nishi, E., Ten Hove, H.A. and Rzhavsky, A.V. 2001. Life-history patterns in serpulimorph polychaetes: Ecological and evolutionary perspectives. Oceanogr. Mar. Biol. Annu. Rev. 39: 1-101.

LaBarbera, M. 1984. Feeding currents and particle capture mechanisms in suspension feeding animals. Am. Zool. 24: 71-84.

Lafrance, M., Cliché, G., Haugum, G.A. and Guderley, H. 2003. Comparison of cultured and wild sea scallops *Placopecten magellanicus*, using behavioral responses and morphometric and biochemical indices. Mar. Ecol. Prog. Ser. 250: 183-195.

Lambert, D.M. and Harris, L.G. 2000. Larval settlement of the green sea urchin, *Strongylocentrotus droebachiensis*, in the southern Gulf of Maine. Invertebr. Biol. 119(4): 403-409.

Lambert, J. 1994. Bivalve molluscs (Stimpson's surfclam, softshell clam and razor clam): their fisheries and development on the coasts of Quebec. p. 82-91. *In:* Savard, L. (ed.). Status report on invertebrates 1993: Crustaceans and molluscs on the Quebec coast and northern shrimp in the Estuary and Gulf of St. Lawrence. Can. Manuscr. Rep. Fish. Aquat. Sci. 2257.

Lambert, J. and Goudreau, P. 1996. Performance of the New England hydraulic dredge for the harvest of Stimpson's surfclams (*Mactromeris polynyma*). Can. Ind. Rep. Fish. Aquat. Sci. 235. 28 p.

Lambert, W.J., Levin, P.S. and Berman, J. 1992. Changes in the structure of a New England (U.S.A.) kelp bed: the effects of an introduced species? Mar. Ecol. Prog. Ser. 88: 303-307.

Landers, W.S. 1976. Reproduction and early development of the ocean quahog, *Arctica islandica*, in the laboratory. Nautilus 90: 88-92.

Lane, C.E., Mayes, C., Druehl, L.D., Saunders, G.W. 2006. A multigene molecular investigation of the kelp (Laminariales, Phaeophyceae) supports substantial taxonomic re-organization. J. Phycol. 42: 493–512.

Langton, R.W. and Robinson, W.E. 1990. Faunal associations on scallop grounds in the western Gulf of Maine. J. Exp. Mar. Biol. Ecol. 144: 157-171.

Larsen, P.F. and Lee, R.M. 1978. Observations on the abundance, distribution and growth of postlarval sea scallops, *Placopecten magellanicus*, on Georges Bank. Nautilus 92(3): 112-116.

Lass, S., Tarling, G.A., Virtue, P., Matthews, J.B.L., Mayzaud, P. and Buchholz, F. 2001. On the food of northern krill *Meganyctiphanes norvegica* in relation to its vertical distribution. Mar. Ecol. Prog. Ser. 214: 177-200.

Last, K.S. 2003. An actograph and its use in the study of foraging behaviour in the benthic polychaetes, *Nereis virens* Sars. J. Exp. Mar. Biol. Ecol. 287(2): 237-248.

Last, K.S. and Olive, P.J.W. 2004. Interaction between photoperiod and an endogenous seasonal factor in influencing the diel locomotor activity of the benthic polychaetes *Nereis virens* Sars. Biol. Bull. 206(2): 103-112.

Lauzon-Guay, J.-S., Scheibling, R.E., 2007. Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature. Mar. Biol. 151, 2109-2118.

Lavalli, K.L. and Barshaw, D.E. 1986. Burrows protect postlarval lobsters *Homarus americanus* from predation by the non-burrowing cunner *Tautogolabrus adspersus*, but not from the burrowing mud crab *Neopanope texani*. Mar. Ecol. Prog. Ser. 32: 13-16.

Lavalli, K.L. and Barshaw, D.E. 1989. Post-larval American lobsters (*Homarus americanus*) living in burrows may be suspension feeding. Mar. Freshw. Behav. Phy. 15: 255-264.

Lavoie, D., Simard, Y. and Saucier, F.J. 2000. Aggregation and dispersion of krill at channel heads and shelf edges: the dynamics in the Saguenay-St. Lawrence Marine Park. Can. J. Fish. Aquat. Sci. 57: 1853-1869.

Lawrence, J.M. 1975. On the relationships between marine plants and sea urchins. Oceanogr. Mar. Biol. Ann. Rev. 13; 213-286.

Lawson, J.W. and Hobson, K.A. 2000. Diet of harp seals (*Pagophilus groenlandicaus*) in nearshore northeast Newfoundland: Inferences from stable-carbon (delta C-13) and nitrogen (delta N-15) isotope analyses. Mar. Mamm. Sci. 16(3): 578-591.

Lawton, P. and K.L. Lavalli. 1995. Postlarval, juvenile, adolescent and adult ecology. p. 47-88. *In* J.R. Factor (ed.). Biology of the lobster *Homarus americanus*. Academic Press, San Diego, CA.

Lazzari, M.A. 2002. Epibenthic fishes and decapod crustaceans in northern estuaries: A comparison of vegetated and unvegetated habitats in Maine. Estuaries 25(6A): 1210-1218.

Legault, C. and Himmelman, J.H. 1993. Relation between escape behaviour of benthic marine invertebrates and the risk of predation. J. Exp. Mar. Biol. Ecol. 170: 55-74.

Lehtonen, K.K., Leiniö, S., Schneider, R. and Leivuori, M. 2003. Biomarkers of pollution effects in the bivalves *Mytilus edulis* and *Macoma balthica* collected from two areas in the southern coast of Finland (Baltic Sea). ICES CM 2003/M:02. 17 p.

Lemire, M. and Himmelman, J.H. 1996. Relation of food preference to fitness for the green sea urchin, *Strongylocentrotus droebachiensis*. Mar. Biol. 127: 73-78.

Lesser, M.P., Witman, J.D. and Sebens, K.P. 1994. Effects of flow and seston availability on scope for growth of benthic suspension-feeding invertebrates from the Gulf of Maine. Biol. Bull. 187: 319-335.

Levin, P.S., Coyer, J.A., Petrik, R. and Good, T.P. 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83(11): 3182-3193.

Lewis, C., Olive, P.J.W. and Bentley, M.G. 2003. Pre-emptive competition as a selective pressure for early reproduction in the polychaetes *Nereis virens*. Mar. Ecol. Prog. Ser. 254: 199-211.

Lewis, C., Olive, P.J.W., Bentley, M.G. and Watson, G. 2002. Does seasonal reproduction occur at the optimal time for fertilization in the polychaetes *Arenicola marina* L. and *Nereis virens* Sars? Invertebr. Reprod. Develop. 41(1-3): 61-71.

Lewis, C.V.W., Weinberg, J.R. and Davis, C.S. 2001. Population structure and recruitment of the bivalve *Arctica islandica* (Linnaeus, 1767) on Georges Bank from 1980-1999. J. Shellfish Res. 20(3): 1135-1144.

Liao, Y.Y. and Lucas, M.C. 2000. Diet of the common wolfish *Anarhichas lupus* in the North Sea. J. Mar. Biol. Assoc. U.K. 80(1): 181-182.

Lick, R. and Piatkowski, U. 1998. Stomach contents of a northern bottlenose whale (*Hyperoodon ampullatus*) stranded at Hiddensee, Baltic Sea. J. Mar. Biol. Assoc. U.K. 78: 643-650.

Liljebladh, B. and Thomasson, M.A. 2001. Krill behaviour as recorded by acoustic doppler current profilers in the Gullmarsfjord. J. Mar. Syst. 27(4): 301-313.

Linnane, A., Ball, B., Mercer, J.P., Browne, R., van der Meeren, G., Ringvold, H., Bannister, C., Mazzoni, D. and Munday, B. 2001. Searching for the early benthic phase (EBP) of the European lobster: a trans-European study of cobble fauna. Hydrobiologia 465: 63-72.

Liyanapathirana, C.M. 2001. Quality characteristics of green sea urchin (*Strongylocentrotus droebachiensis*) gonads as affected by the season and dietary factors. M.Sc. Thesis, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 268 p.

Logan, A. 1988. A sublittoral hard substrate epibenthic community below 30 m in Head Harbour Passage, New Brunswick, Canada. Estuar. Coast. Shelf Sci. 27(4): 445-459.

Loomis, S.H. 1995. Freezing tolerance of marine invertebrates. Oceanogr. Mar. Biol. Annu. Rev. 33: 337-350.

Lovrich, G.A., Sainte-Marie, B. and Smith, B.D. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Can. J. Zool. 73: 1712-1726.

Lowe, D.M., Moore, M.N. and Bayne, B.L. 1982. Aspects of gametogenesis in the marine mussel *Mytilus edulis* L. J. Mar. Biol. Assoc. U.K. 62: 133-145.

Lubinsky, I. 1980. Marine bivalve molluscs of the Canadian central and eastern arctic: faunal composition and zoogeography. Can. Bull. Fish. Aquat. Sci. 207. 111 p.

Lucas, C.H. 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia 451: 229-246.

Lutz, R.A. and Kennish, 1992. Ecology and morphology of larval and early postlarval mussels. p. 53-86. *In* Gosling, E. (ed.). The Mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Developments in Aquaculture and Fisheries 25. Elsevier.

Lydersen, C., Gjertz, I. and Weslawski, J.M. 1989. Stomach contents of autumn-feeding marine vertebrates from Hornsund, Svalbard. Polar Rec. 25(153): 107-114.

Macalaster, E.G. 1981. Dark-water octopus. Sea Front., March-April 1981: 79-81.

MacDonald, B.A. and Thompson, R.J. 1985a. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. I. Growth rates of shell and somatic tissue. Mar. Ecol. Prog. Ser. 25: 279-294.

MacDonald, B.A. and Thompson, R.J. 1985b. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. II. Reproductive output and total production. Mar. Ecol. Prog. Ser. 25: 295-303.

MacDonald, B.A. and Thompson, R.J. 1986. Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. III. Physiological ecology, the gametogenic cycle and scope for growth. Mar. Biol. 93: 37-48.

MacKay, A.A. 1977. *Myxicola infundibulum*. Ecology in the Bay of Fundy. Final report to the Res. Dev. Br., New Brunswick Dept. Fish, Fredericton, N.B., by Marine Res. Assoc. Ltd., Deer Island, N.B. 23 p.

Mackenzie, C.L., Jr., Radosh, D. and Reid, R.N. 1984. Sediment preferences and mortality in young surfclams (*Spisula solidissima* Dillwyn). Abstracts, 1984 Annual Meeting, June 25-28, National Shellfish Association, Tampa, Florida. 40 p.

Macy, W.K., III. 1982. Feeding patterns of the long-finned squid, *Loligo pealeii*, in New England waters. Biol. Bull. 162: 28-38.

Macy, W.K. 1995. Recruitment of long-finned squid in New England (U.S.A.) waters. ICES CM 1995/K:35. Shellfish Committee. 17 p.

Madin, L.P., Bollens, S.M., Horgan, E., Butler, M., Runge, J., Sullivan, B.K., Klein-MacPhee, G., Durbin, E., Durbin, A.G., Van Keurin, D., Plourde, S., Bucklin, A. and Clarke, M.E. 1996. Voracious planktonic hydroids: unexpected predatory impact on a coastal marine ecosystem. Deep Sea Res. (II Top. Stud. Oceanogr.) 43(7-8): 1823-1829.

Mahon, R., Brown, S.K., Zwanenburg, K.C.T., Atkinson, D.B., Buja, K.R., Claflin, L., Howell, G.D., Monaco, M.E., O'Boyle, R.N. and Sinclair, M. 1998. Assemblages and biogeography of demersal fishes of the east coast of North America. Can. J. Fish. Aquat. Sci. 55: 1704-1738.

Malatesta, R.J., Auster, P.J. and Carlin, B.P. 1992. Analysis of transect data for microhabitat correlations and faunal patchiness. Mar. Ecol. Prog. Ser. 87: 189-195.

Mallet, A.L. and Myrand, B. 1995. The culture of the blue mussel in Atlantic Canada. p. 255-296. *In* Boghen, A.D. (ed.). Cold-water Aquaculture in Atlantic Canada. The Canadian Institute for Research on Regional Development. Sackville, NB.

Manderson, J.P., Phelan, B.A., Stoner, A.W. and Hilbert, J. 2000. Predator-prey relations between age-1+ summer flounder (*Paralichthys denatus*, Linneus) and age-0 winter flounder (*Pseudopleuronectes americanus*, Walbaum): predator diets, prey selection and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol. 251: 17-39.

Mangel, M. and Nicol, S. 2000. Krill and the unity of biology. Can. J. Fish. Aquat. Sci. 57(Suppl. 3): 1-5.

Mangold, K. 1987. Reproduction. p. 157-219. *In* Boyle, P.R. (ed.) Cephalopod life cycles. Volume II. Comparative reviews. Academic Press, London.

Mann, K.H. 1992. The extent and importance of rockweed as a habitat for finfish, shellfish and other species. CAFSAC Res. Doc. 92/116 8 p.

Mann, K.H., 2000. Ecology of coastal waters: with implications for management. Blackwell Science, Malden, Mass., 406 p.

Mann, R. 1979. The biology of the ocean quahog, *Arctica islandica*. Sea Grant Program Summary, 1980-81. Annual Sea Grant Report Woods Hole Oceanographic Institution. p. 5-6.

Mann, R. 1985. Seasonal changes in the depth distribution of bivalve larvae on the southern New England shelf. J. Shellfish Res. 2: 57-64.

Mann, R. 1990. Larval ecology of *Arctica islandica* on the inner continental shelf of the eastern United States. Abstracts: 1990 Annual Meeting, April 1-5, National Shellfisheries Association, Williamsburg, Virginia. 464 p.

Mann, R. and Wolf, C.C. 1983. Swimming behaviour of larvae of the ocean quahog *Arctica islandica* in response to pressure and temperature. Mar. Ecol. Prog. Ser. 13: 211-218.

Margoński, P. and Horbowa, K. 1994. Co-occurrence of medusae and cod eggs in the Bornholm Basin. ICES CM 1994/J:18. 7 p.

Marine Biological Association of the U.K. 2003. Biodiversity and Conservation. Marine Life Information Network. http://www.marlin.ac.uk/sah/species_information.php.

Martel, A., Larrivée, D.H. and Himmelman, J.H. 1986a. Behaviour and timing of copulation and egg-laying in the neogastropod *Buccinum undatum* L. J. Exp. Mar. Biol. Ecol. 96: 27-42.

Martel, A., Larrivée, D.H., Klein, K.R. and Himmelman, J.H. 1986b. Reproductive cycle and seasonal feeding activity of the neogastropod *Buccinum undatum*. Mar. Biol. 92: 211-221.

Martinez, P., Sanjuan, A. and Guerra, A. 2002. Identification of *Illex coindetii*, *I. illecebrosus* and *I. argentinus* (Cephalopoda: Ommastrephidae) throughout the Atlantic Ocean; by body and beak characters. Mar. Biol. 141: 131-143.

Martinussen, M.B. and Baamstedt, U. 2001. Digestion rate in relation to temperature of two gelatinous planktonic predators. Sarsia 86(1): 21-35.

Mathieson, S. and Berry, A.J. 1997. Spatial, temporal and tidal variation in crab populations in the Forth Estuary, Scotland. J. Mar. Biol. Assoc. U.K. 77: 167-183.

Matsakis, S. and Conover, R.J. 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can. J. Fish. Aquat. Sci. 48: 1419-1430.

Matsumoto, G.I. and Harbison, G.R. 1993. *In situ* observations of foraging, feeding and escape behavior in three orders of oceanic ctenophores: Lobata, Cestida and Beroida. Mar. Biol. 117: 279-287.

Matthews, J.B.L., Buchholz, F., Saborowski, R., Tarling, G.A., Dallot, S. and Labat, J.P. 1999. On the physical oceanography of the Kattegat and Clyde Sea area, 1996-98, as background to ecophysiological studies on the planktonic crustacean, *Meganyctiphanes norvegica* (Euphausiacea). Helgol. Mar. Res. 53: 70-84.

Mattila, J., Chaplin, G., Eilers, M.R., Heck, K.L., O'Neal, J.P. and Valentine, J.F. 1999. Spatial and diurnal distribution of invertebrate and fish fauna of a *Zostera marina* bed and nearby unvegetated sediments in Damariscotta River, Maine (U.S.A.). J. Sea Res. 41(4): 321-332.

Mauchline, J. 1966. The biology of *Thysanoessa raschii* (M. Sars), with a comparison of its diet with that of *Meganyctiphanes norvegica* (M. Sars). p. 493-510. *In* H. Barnes (ed.). Some Contemporary Studies in Marine Science. George Allen and Unwin Ltd., London.

Maurer, R.O. and Bowman, R.E. 1985. Food consumption of squids (*Illex illecebrosus* and *Loligo pealeii*) off the Northeastern United States. Sci. Counc. Stud. NAFO 9: 117-124.

Maxwell, M.R., Macy, W.K. and Hanlon, R.T. 1998. Evidence for multiple spawning by squids (*Loligo pealeii*) in captivity. Biol. Bull. 195: 225-226.

McDermott, J.J. 2001. Symbionts of the hermit crab *Pagurus longicarpus* Say, 1817 (Decapoda: Anomura): New observations from New Jersey waters and a review of all known relationships. Proc. Biol. Soc. Wash. 114(3): 624-639.

McEdward, L.R. and Chia, F-S. 1991. Size and energy content of eggs from echinoderms with pelagic lecithotrophic development. J. Exp. Mar. Biol. Ecol. 147: 95-102.

Meade, J.D., Hamoutene, D., Power, F.M., Fancey, L.L. and Payne, J.F. 2000. Marine bivalve data from a site contaminated with copper mine tailings and a reference site in Notre Dame Bay, Newfoundland. Can. Data Rep. Fish. Aquat. Sci. 1062. 21 p.

Medeiros-Bergen, D.E. and Miles, E. 1997. Recruitment in the holothurian *Cucumaria frondosa* in the Gulf of Maine. Invertebr. Reprod. Develop. 31(1-3): 123-133.

Medeiros-Bergen, D.E., Olson, R.R., Conroy, J.A. and Kocher, T.D. 1995. Distribution of holothurian larvae determined with species-specific genetic probes. Limnol. Oceanogr. 40(7): 1225-1235.

Medcof, J.C. 1958. Stock taking of molluscan shellfish resources and prospects for improvement. Fish. Res. Board Can., Atlantic Progress Reports. 71: 21-26.

Meidel, S.K. and Scheibling, R.E. 1998. Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada. Mar. Biol. 131: 461-478.

Meidel, S.K. and Schleibling, R.E. 2001. Variation in egg spawning among subpopulations of sea urchins *Strongylocentrotus droebachiensis*: a theoretical approach. Mar. Ecol. Prog. Ser. 213: 97-110.

Meidel, S.K., Scheibling, R.E. and Metaxas, A. 1999. Relative importance of parental and larval nutrition on larval development and metamorphosis of the sea urchin *Strongylocentrotus droebachiensis*. J. Exp. Mar. Biol. Ecol. 240: 161-178.

Meidel, S.K. and Yund, P.O. 2001. Egg longevity and time-integrated fertilization in a temperate sea urchin (*Strongylocentrotus droebachiensis*). Biol. Bull. 201(1): 84-94.

Mercier, A., Pelletier, É. and Hamel, J.-F. 1998. Response of temperate sea anemones to butyltin contamination. Can. J. Fish. Aquat. Sci. 55: 239-245.

Meyer, T.L. Anderson, E.L., Ropes, J.W. and Phoel, W.C. 1987. Underwater observations of a surfclam, *Spisula solidissima* (Dillwyn), community and the relative efficiency of a prototype airlift clam sampler. Mar. Fish. Rev. 49(4): 23-33.

Michalsen, K. and Nedreaas, K.H. 1998. Food and feeding of Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum) in the Barents Sea and east Greenland waters. Sarsia 83: 401-407.

Michaud, G. and Ferron, J. 1990. Sélection des proies par quatre espèces d'oiseaux limicoles (Charadrii) de passage dans l'estuaire du Saint-Laurent lors de la migration vers le sud. Can. J. Zool. 68: 1154-1162.

Miles, E. 1995. Population distribution of *Cucumaria frondosa* along the New Hampshire coast: where is everyone? Twenty-Third Benthic Ecology Meeting, New Brunswick, New Jersey.

Miller, J.A. and Shanks, A.L. 2004. Ocean-estuary coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae. Mar. Ecol. Prog. Ser. 271: 267-279.

Miller, R.J. and O'Keefe, P.G. 1981. Seasonal and depth distribution, size and molt cycle of the spider crabs, *Chionoecetes opilio*, *Hyas araneus* and *Hyas coarctatus* in a Newfoundland Bay. Can. Tech. Rep. Fish. Aquat. Sci. 1003. 18 p.

Milne, W.R. and Corey, S. 1986. Distributional patterns of the ctenophores *Pleurobrachia pileus* and *Beroe cucumis* in the Bay of Fundy region, Canada. Can. J. Zool. 64: 2639-2644.

Minor, M.A. and Scheibling, R.E. 1997. Effects of food ration and feeding regime on growth and reproduction of the sea urchin *Strongylocentrotus droebachiensis*. Mar. Biol. 129: 159-167.

Miron, G.Y. and Desrosiers, G.L. 1990. Distributions and population structures of two intertidal estuarine polychaetes in the lower St. Lawrence Estuary, with special reference to environmental factors. Mar. Biol. 105: 297-306. ix + 29 p.

Miron, G., Desrosiers, G., Retière, C. and Lambert, R. 1991. Dispersion and prospecting behaviour of the polychaete *Nereis virens* (Sars) as a function of density. J. Exp. Mar. Biol. Ecol. 145: 65-77.

Miron, G., Landry, T. and MacNair, N. 2002. Predation potential by various epibenthic organisms on commercial bivalve species in Prince Edward Island: preliminary results. Can. Tech. Rep. Fish. Aquat. Sci. 2392.

Miyake, H., Iwao, K. and Kakinuma, Y. 1997. Life history and environment of *Aurelia aurita*. South Pacific Study 17(2): 273-285.

Modlin, R.F. 1980. The life cycle and recruitment of the sand shrimp, *Crangon septemspinosa*, in the Mystic River Estuary, Connecticut. Estuaries 3(1): 1-10.

Möller, H. 1979. Significance of coelenterates in relation to other plankton organisms. Meeresforschung. 27: 1-18, Ref. L. Baltic Fish Committee. 11 p.

Moody, K.E. and Steneck, R.S. 1993. Mechanisms of predation among large decapod crustaceans of the Gulf of Maine: functional vs. phylogenetic patterns. J. Exp. Mar. Biol. Ecol. 168: 111-124.

Moore, D.S., Miller, R.J. and Meade, L.D. 1986. Survey of shallow benthic habitat: Eastern shore and Cape Breton Island, Nova Scotia. Can. Res. Rep. Fish. Aquat. Sci. 1546. 49 p.

Morissette, S. and Himmelman, J.H. 2000a. Subtidal food thieves: interactions of four invertebrate kleptoparasites with the sea star *Leptasterias polaris*. Anim. Behav. 60: 531-543.

Morissette, S. and Himmelman, J.H. 2000b. Decision of the asteroid *Leptasterias polaris* to abandon its prey when confronted with its predator, the asteroid *Asterias vulgaris*. J. Exp. Mar. Biol. Ecol. 252: 151-157.

Moriyasu, M. and Lanteigne, C. 1998. Embryo development and reproductive cycle in the snow crab, *Chionoecetes opilio* (Crustacea: Majidae), in the southern Gulf of St. Lawrence, Canada. Can. J. Zool. 76: 2040-2048.

Moriyasu, M., Landsburg, W., Wade, E. and Maynard, D.R. 1999. The role of an estuary environment for regeneration of claws in the American lobster, *Homarus americanus* H. Milne Edwards, 1837 (Decapoda). Crustaceana 72(4): 415-433.

Motnikar, S. and Hotton, J. 1995. Analyses biotechniques d'enchatillons de mye (*Mya arenaria*), de mactre de Stimpson (*Mactromeris polynyma*) et de couteau (*Ensis directus*) provenant de producteurs Quebecois. MAPA-Pecheries, DRST-Doc. Rech. 95/05.

Mullen, D.M. and Moring, J.R. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): Sea Scallop. Fish Wildl. Serv., U.S. Dep. Int. Biol. Rep. 82 (11.67) TR EL-82-4. 13 p.

Mutlu, E. 2001. Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. Mar. Biol. 138: 329-339.

Nadeau, M. and Cliche, G. 1998. Predation of juvenile sea scallops (*Placopecten megellanicus*) by crabs (*Cancer irroratus* and *Hyas* sp.) and starfish (*Asterias vulgaris*, *Leptasterias polaris* and *Crossaster papposus*). J. Shellfish Res. 17(4): 905-910.

Naidu, K.S. 1970. Reproduction and breeding cycle of the giant scallop *Placopecten magellanicus* (Gmelin) in Port au Port Bay, Newfoundland. Can. J. Zool. 48: 1003-1012.

Naidu, K.S. 1988. Estimating mortality in the Iceland scallop, *Chlamys islandica* (O.F. Müller). J. Shellfish Res. 7(1): 61-71.

Naidu, K.S. and Cahill, F.M. 1989. The quest for Iceland scallops, *Chlamys islandica* (O.F. Müller) on the Grand Bank, NAFO Division 3LNO. Can. Atl. Fish. Sc. Adv. Comm. Res. Doc. 89/12. 31 p.

Naidu, K.S., Lawrence, J.M., Cahill, F.M. and Seward, E.M. 1999. An epidemic of starfish on scallop grounds. Book of Abstracts: 12th International Pectinid Workshop, Bergen, Norway, 5-11 May 1999.

Navarro, J.M. and Thompson, R.J. 1995. Seasonal fluctuations in the size spectra, biochemical composition and nutritive value of the seston available to a suspension-feeding bivalve in a subarctic environment. Mar. Ecol. Prog. Ser. 125: 95-106.

Navarro, J.M. and Thompson, R.J. 1997. Biodeposition by the horse mussel *Modiolus modiolus* (Dillwyn) during the spring diatom bloom. J. Exp. Mar. Biol. Ecol. 209: 1-13.

Nelson, K., Hedgecock, D. and Borgeson, W. 1988. Factors influencing egg extrusion in the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 45: 797-804.

Nesis, K.N. 2001. West-Arctic and East-Arctic distributional ranges of cephalopods. Sarsia 86: 1-11.

Newell, C.R. and Hidu, H. 1982. The effects of sediment type on growth rate and shell allometry in the soft shelled clam *Mya arenaria* L. J. Exp. Mar. Biol. Ecol. 65: 285-295.

Newell, C.R. and Hidu, H. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): Softshell clam. Fish Wildl. Serv., Biol. Rep. 82 (11.53). U.S. Army Corps of Eng., TR EL-82-4. 17 p.

Nicol, S. 2003. Living krill, zooplankton and experimental investigations: A discourse on the role of krill and their experimental study in marine ecology. Mar. Freshw. Behav. Phy. 36(4): 191-205.

Nielsen, C. 2002. Ciliary filter-feeding structures in adult and larval gymnolaemate bryozoans. Invertebr. Biol. 121(3): 255-261.

Nilssen, K.T., Haug, T. and Potelov, V. 1991. Field studies of harp seal *Phoca groenlandica* distribution and feeding ecology in the Barents Sea in September 1990. ICES CM 1991/N:3. Marine Mammals Committee. 23 p.

Norrbin, M.F., Davis, C.S. and Gallager, S.M. 1996. Differences in fine-scale structure and composition of zooplankton between mixed and stratified regions of Georges Bank. Deep Sea Res. (II Top. Stud. Oceanogr.) 43(7-8): 1905-1924.

Oba, T. and Goshima, S. 2004. Temporal and spatial settlement patterns of sympatric hermit crabs and the influence of shell resource availability. Mar. Biol. 144: 871-879.

O'Dor, R.K. and Balch, N. 1985. Properties of *Illex illecebrosus* egg masses potentially influencing larval oceanographic distribution. Sci. Coun. Stud. NAFO 9: 69-76.

O'Dor, R.K., Balch, N., Foy, E.A., Hirtle, R.W.M., Johnson, D.A. and Amaratunga, T. 1982. Embryonic development of the squid, *Illex illecebrosus* and the effect of temperature on development rates. J. Northwest Atl. Fish. Sci. 3: 41-45.

O'Dor, R.K. and Macalaster, E.G. 1983. *Bathypolypus arcticus*. p. 401-410. *In* Boyle, P.R. (ed.). Cephalopod Life Cycles, Volume I, Species Accounts. Academic Press. London.

Oganesyan, S.A. 1994. Biological characteristics and time of Icelandic scallop (*Chlamys islandica*) spawning on the Kanin Bank and off the Bear Island-Spitsbergen. ICES CM 1994/K:45. Shellfish Committee. 10 p.

Ojeda, F.P. and Dearborn, J.H. 1989. Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: seasonal and bathymetric distribution. Mar. Ecol. Prog. Ser. 57: 147-161.

Ojeda, F.P. and Dearborn, J.H. 1991. Feeding ecology of benthic mobile predators: experimental analyses of their influences in rocky subtidal communities of the Gulf of Maine. J. Exp. Mar. Biol. Ecol. 149: 13-44.

Okamura, B. and Partridge, J.C. 1999. Suspension feeding adaptations to extreme flow environments in a marine bryozoan. Biol. Bull. 196: 205-215.

Olive, P.J.W. 1999. Polychaete aquaculture and polychaete science: a mutual synergism. Hydrobiologia 402: 175-183.

Olivier, M., Desrosiers, G., Retiere, C. and Brethes, J.-C. 1993. Spatial and temporal feeding variations on an estuarine polychaete, *Nereis virens* (lower St. Lawrence Estuary, Quebec). Vie milieu, Paris 43(1): 1-12.

Olmi, E.J., III and Lipcius, R.N. 1991. Predation on postlarvae of the blue crab *Callinectes sapidus* Rathbun by sand shrimp *Crangon septemspinosa* Say and grass shrimp *Palaemonetes pugio* Holthius. J. Exp. Mar. Biol. Ecol. 151: 169-183.

Olsgard, F. 1999. Effects of copper contamination on recolonisation of subtidal marine soft sediments – an experimental field study. Mar. Poll. Bull. 38(6): 448-462.

Orejas, C., Gili, J.M., Alva, V. and Arntz, W. 2000. Predatory impact of an epiphytic hydrozoan in an upwelling area in the Bay of Coliumo (Dichato, Chile). J. Sea Res. 44(3-4): 209-220.

Orlov, D.V. 1996. The role of larval settling behaviour in determination of the specific habitat of the hydrozoan *Dynamena pumila* (L.). Larval settlement in *Dynamena pumila* (L.). J. Exp. Mar. Biol. Ecol. 208: 73-85.

Orr, D.C., Parsons, D.G., Veitch, P.J. and Sullivan, D.J. 2002. Northern shrimp (*Pandalus borealis*) off Baffin Island, Labrador and northeastern Newfoundland-second interim review. DFO Can. Sci. Advis. Sec. Res. Doc. 2002/035. 50 p.

Orr, D.C., Veitch P.J. and Sullivan D.J. 2005. An update of information pertaining to northern shrimp (*Pandalus borealis*, Kroyer) and groundfish in NAFO Divisions 3LNO. Sci. Counc. Res. Doc. NAFO 05/88. 59 p.

Östman, C. 1997. Abundance, feeding behaviour and nematocysts of scyphopolyps (Cnidaria) and nematocysts in their predator, the nudibranch *Coryphella verrucosa* (Mollusca). Hydrobiologia 355: 21-28.

Ouellet, P. and Allard, J.-P. 2002. Seasonal and interannual variability in larval lobster *Homarus americanus* size, growth and condition in the Magdalen Islands, southern Gulf of St. Lawrence. Mar. Ecol. Prog. Ser. 230: 241-251.

Ouellet, P., Allard, J.-P. and St. Pierre, J.-F. 1994. Distribution des larves d'invertébrés decapods (Pandalidae, Majidae) at des oeufs et larves de poisons dans le nord du golfe du Saint-Laurent en mai et juin de 1985 à 1987 et 1991-1992. Rapp. Tech. Can. Sci. Halieut. Aquat. 2019: viii + 60 p.

Oug, E. 2001. Polychaetes in intertidal rocky and sedimentary habitats in the region of Tromso, northern Norway. Sarsia 86(1): 75-83.

Overholtz, W.J., Link, J.S. and Suslowicz, L.E. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern U.S.A. shelf ecosystem with some fishery comparisons. ICES J. Mar. Sci. 57: 1147-1159.

Packer, D.B., Watling, L. and Langton, R.W. 1994. The population structure of the brittle star *Ophiura sarsi* Lütken in the Gulf of Maine and its trophic relationship to American plaice (*Hippoglossoides platessoides* Fabricius). J. Exp. Mar. Biol. Ecol. 179: 207-222.

Pagès, F., González, H.E. and González, S.R. 1996. Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae). Mar. Ecol. Prog. Ser. 139: 69-77.

Paille, N., Sainte-Marie, B. and Brethes, J.C. 2002. Behaviour, growth and survival of stage V lobsters (*Homarus americanus*) in relation to shelter availability and lobster density. Mar. Freshw. Behav. Phy. 35(4): 203-219.

Palma, A.T., Steneck, R.S. and Wilson, C.J. 1999. Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. J. Exp. Mar. Biol. Ecol. 241: 107-136.

Palma, A.T., Wahle, R.A. and Steneck, R.S. 1998. Different early post-settlement strategies between American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* in the Gulf of Maine. Mar. Ecol. Prog. Ser. 162: 215-225.

Pape-Lindstrom, P.A., Feller, R.J., Stancyk, S.E. and Woodin, S.A. 1996. Sublethal predation on brittlestars: What is this and why is it relevant? Abstract: Twenty-fourth Annual Benthic Ecology Meeting, Columbia, South Carolina, March 7-10, 1996. p.64.

Parsons, D.G. and Tucker, G.E. 1986. Fecundity of northern shrimp, *Pandalus borealis* (Crustacea, Decapoda), in areas of the northwest Atlantic. Fish. Bull. 84: 549-558.

Parsons, D.G. and Fréchette, J. 1989. Fisheries for northern shrimp (*Pandalus borealis*) in the northwest Atlantic from Greenland to the Gulf of Maine. p. 63-85. *In* Caddy, J.F. (ed.). Marine Invertebrate Fisheries: Their Assessment and Management. John Wiley & Sons, Inc.

Parsons, G.J., Shumway, S.E., Kuenster, S. and Gryska, A. 2002. Polyculture of sea scallops (*Placopecten magellanicus*) suspended from salmon cages. Aquacult. Int. 10: 65-77.

Patil, J.S. and Anil, A.C. 2000. Epibiotic community of the horseshoe crab *Tachypleus gigas*. Mar. Biol. 136: 699-713.

Paz, J., Casas, J.M. and Perez-Gandaras, G. 1993. The feeding of cod (*Gadus morhua*) on Flemish Cap, 1989-90. Sci. Coun. Stud. NAFO 19: 41-50.

Pearce, C.M., Daggett, T.L. and Robinson, S.M. 2004. Effect of urchin size and diet on gonad yield in the green sea urchin (*Strongylocentrotus droebachiensis*). Aquaculture 233: 337-367.

Pearce, C.M. and Scheibling, R.E. 1990. Induction of settlement and metamorphosis in the sand dollar *Echinarachnius parma*: evidence for an adult-associated factor. Mar. Biol. 107: 363-369.

Pedersen, O.P., Aschan, M., Rasmussen, T., Tande, K.S. and Slagstad, D. 2003. Larval dispersal and mother populations of *Pandalus borealis* investigated by a Lagrangian particle-tracking model. Fish. Res. 65(1-3): 173-190.

Pellerin-Massicotte, J. 1994. Validation and calibration of the responses of biomarkers in an estuarine ecosystem. ICES CM 1994/K:17. Shellfish Committee. 14 p.

Penney, R.W. and Mills, T.J. 2000. Bioeconomic analysis of a sea scallop, *Placopecten magellanicus*, aquaculture production system in Newfoundland, Canada. J. Shellfish Res. 19(1): 113-124.

Pennington J.T. 1985. The ecology of fertilization of echinoid eggs: the consequences of sperm dilution, adult aggregation and synchronous spawning. Biol. Bull. 169: 417-430.

Penton, P.M. 2003. A subtidal investigation of nudibranchs associated with the hydroids *Obelia* and *Tubularia* in Bonne Bay, Newfoundland. Hons. Diss. (B.Sc.), Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 42 p.

Pepin, P. and Shears, T.H. 1997. Variability and capture efficiency of bongo and Tucker trawl samplers in the collection of ichthyoplankton and other macrozooplankton. Can. J. Fish. Aquat. Sci. 54: 765-773.

Pérez, E., Blasco, J. and Solé, M. 2004. Biomarker responses to pollution in two invertebrate species: *Scrobiccularia plana* and *Nereis diversicolor* from the Cádiz bay (SW Spain). Mar. Environ. Res. 58: 275-279.

Perez, J.A. and O'Dor, R.K. 2000. Critical transitions in early life histories of short-finned squid, *Illex illecebrosus* as reconstructed from gladius growth. J. Mar. Biol. Assoc. U.K. 80: 509-514.

Perez, J.A., O'Dor, R.K., Beck, P. and Dawe, E.G. 1996. Evaluation of gladius dorsal surface structure for age and growth studies of the short-finned squid, *Illex illecebrosus* (Teuthoidea: Ommastrephidae). Can. J. Fish. Aquat. Sci. 53: 2837-2846.

Perkins, H.C. 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). Fish. Bull. 70: 95-99.

Petersen, S. 1995. The embryonic development of *Hyas araneus* L. (Decapoda, Majidae): effects of temperature. Sarsia 80: 193-198.

Petraitis, P.S. 1982. Occurrence of random and directional movements in the periwinkle, *Littorina littorea* (L.). J. Exp. Mar. Biol. Ecol. 59: 207-217.

Petraitis, P.S. 1983. Grazing patterns of the periwinkle and their effect on sessile intertidal organisms. Ecology 64: 522-533.

Petraitis, P.S. 1990. Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. Oecologia 83: 405-413.

Petraitis, P.S. 1995. Are periwinkles (*Littorina littorea*) hyenas on the plains of the intertidal shore? Twenty-Third Benthic Ecol. Meeting. Rutgers-the State University, New Brunswick, NJ. Inst, Marine Coastal Sciences.

Petraitis, P.S. 2002. Effects of intraspecific competition and scavenging on growth of the periwinkle *Littorina littorea*. Mar. Ecol. Prog. Ser. 236: 179-187.

Pezzack, D.S. and D.R. Duggan. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 43: 2206-2211.

Phelan, B.A., Manderson, J.P., Stoner, A.W. and Bejda, A.J. 2001. Size-related shifts in the habitat associations of young-of-the-year winter flounder (*Pseudopleuronectes americanus):* field observations and laboratory experiments with sediments and prey. J. Exp. Mar. Biol. Ecol. 257: 297-315.

Piepenburg, D. and Schmid, M.K. 1996. Brittle star fauna (Echinodermata: Ophiuroidea) of the Arctic northwestern Barents Sea: composition, abundance, biomass and spatial distribution. Polar Biol. 16: 383-392.

Pocklington, P. and Tremblay, M.J. 1987. Faunal zones in the northwestern Atlantic based on polychaete distribution. Can. J. Zool. 65: 391-402.

Pohle, G.W. 1991. Larval development of Canadian Atlantic oregoniid crabs (Brachyura: Majidae), with emphasis on *Hyas coarctatus alutaceus* Brandt, 1851 and a comparison with Atlantic and Pacific conspecifics. Can. J. Zool. 69:2717-2737.

Porter, J.S. 2004. Morphological and genetic characteristics of erect subtidal species of *Alcyonidium* (Ctenostomata: Bryozoa). J. Mar. Biol. Assoc. U.K. 84: 243-252.

Porter, J.S., Dyrynda, P.E.J., Ryland, J.S. and Carvalho, G.R. 2001b. Morphological and genetic adaptation to a lagoon environment: a case study in the bryozoan genus *Alcyonidium*. Mar. Biol. 139: 575-585.

Porter, J.S., Ellis, J.R., Hayward, P.J., Rogers, S.I. and Callaway, R. 2002. Geographic variation in the abundance and morphology of the bryozoan *Alcyonidium diaphanum* (Ctenostomata: Alcyonidiidae) in U.K. coastal waters. J. Mar. Biol. Assoc. U.K. 82: 529-535.

Porter, J.S. and Hayward, P.J. 2004. Species of *Alcyonidium* (Bryozoa: Ctenostomata) from Antarctica and Magellan Strait, defined by morphological, reproductive and molecular characters. J. Mar. Biol. Assoc. U.K. 84: 253-265.

Porter, J.S., Hayward, P.J. and Spencer Jones, M.E. 2001a. The identity of *Alcyonidium diaphanum* (Bryozoa: Ctenostomatida). J. Mar. Biol. Assoc. U.K. 81: 1001-1008.

Posgay, J.A. 1979. Population assessment of the Georges Bank sea scallop stocks. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 109-113.

Prena, J., Schwinghamer, P., Rowell, T.W., Gordon, D.C., Jr., Gilkinson, K.D., Vass, W.P. and McKeown, D.L. 1999. Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna. Mar. Ecol. Prog. Ser. 181: 107-124.

Price, K.S., Jr. 1962. Biology of the sand shrimp, *Crangon septemspinosa*, in the shore zone of the Delaware Bay Region. Chesapeake Sci. 3: 244-255.

Pryor, M. and Parsons, G.J. 1999. Larval distribution of blue mussel (*Mytilus edulis* and *M. trossulus*) and predatory starfish (*Asterias vulgaris*) during a 12-hour tidal cycle. Bull. Aquacult. Assoc. Can. 99-4: 37-39.

Pryor, M., Parsons, G.J. and Couturier, C. 1999. Temporal patterns of larval and post-set distributions of blue mussel (*Mytilus edulis* and *M. trossulus*) and starfish (*Asterias vulgaris*) at mussel culture sites in Newfoundland. Bull. Aquacult. Assoc. Can. 99-4: 40-42.

Pulfrich, A. 1996. Attachment and settlement of post-larval mussels (Mytilus edulis L.) in the Schleswig-Holstein Wadden Sea. J. Sea Res. 36: 239-250.

Purcell, J.E. 2003. Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 246: 137-152.

Purcell, J.E. and Arai, M.N. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27-44.

Purcell, J.E. and Sturdevant, M.V. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Mar. Ecol. Prog. Ser. 210: 67-83.

Raby, D., Mingelbier, M., Dodson, J.J., Klein, B., Lagadeuc, Y. and Legendre, L. 1997. Food-particle size and selection by bivalve larvae in a temperate embayment. Mar. Biol. 127: 665-672.

Rangeley, R.W. and Lawton, P. 1999. Spatial scaling of habitat distributions in the American lobster. Abstracts, 1999 Annual Meeting, April 18-22, National Shellfisheries Association, Halifax, Nova Scotia. p. 307.

Raposa, K.B. and Oviatt, C.A. 2000. The influence of contiguous shoreline type, distance from shore and vegetation biomass on nekton community structure in eelgrass beds. Estuaries 23(1): 46-55.

Rathbun, M.J. 1925. The spider crabs of America. Bull. U.S. Natl. Mus. 129: 232-252.

Ray, G.L. 2000. Infaunal assemblages on constructed intertidal mudflats at Jonesport, Maine (U.S.A.). Mar. Poll. Bull. 40(12): 1186-1200.

Read, K.R.H. and Cumming, K.B. 1967. Thermal tolerance of the bivalve molluscs *Modiolus modiolus* L., *Mytilus edulis* L. and *Brachidontes demissus* Dillwyn. Comp. Biochem. Physiol. 22: 149-155.

Reddin, D. 1973. The ecology and feeding habits of the American lobster (*Homarus americanus* Milne-Edwards, 1837) in Newfoundland. M.Sc. Thesis, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland. 83 p.

Reed, C.G. 1991. Bryozoa. p. 85-245. *In* Giese, A.C., Pearse, J.S. and Pearse, V.B. (eds.). Reproduction of Marine Invertebrates. Volume VI: Echinoderms and Lophophorates. The Boxwood Press, Pacific Grove, CA.

Reise, K., Simon, M. and Herre, E. 2001. Density-dependent recruitment after winter disturbance on tidal flats by the lugworm *Arenicola marina*. Helgol. Mar. Res. 55: 161-165.

Reiss, H., Knäuper, S. and Kröncke, I. 2003. Invertebrate associations with gastropod shells inhabited by *Pagurus bernhardus* (Paguridae) – secondary hard substrate increasing biodiversity in North Sea soft-bottom communities. Sarsia 88: 404-414.

Riis, A. and Dolmer, P. 2003. The distribution of the sea anemone *Metridium senile* (L.) related to dredging for blue mussels (*Mytilus edulis* L.) and flow habitat. Ophelia 57(1): 43-52.

Rivard, D., Hendrickson, L.C. and Serchuk, F.M. 1998. Yield estimates for short-finned squid (*Illex illecebrosus*) in SA 3-4 from research vessel survey biomass indices. Sci. Counc. Res. Doc. NAFO 98/75. 4 p.

Robert, G. 1981. Dynamics of an exploited population of bar clam, *Spisula solidissima*. Can. Manuscr. Rep. Fish. Aquat. Sci. 1607. 13 p.

Roberts, M.H., Jr. 1973. Larval development of *Pagurus acadianus* Benedict, 1901, reared in the laboratory (Decapoda, Anomura). Crustaceana 24(3): 303-317.

Robichaud, D.A., Bailey, R.F.J. and Elner, R.W. 1986. The predatory behaviour of cod (*Gadus morhua*) and skate (*Raja radiata*) on crab prey species (*Chionoecetes opilio*, *Hyas araneus* and *H. coarctatus*). ICES CM 1986/G:47. Ref. Demersal Fish Committee Sess. R. 32 p.

Robichaud, D.A., Bailey, R.F.J. and Elner, R.W. 1989. Growth and distribution of snow crab, *Chionoecetes opilio*, in the southeastern Gulf of St. Lawrence. J. Shellfish Res. 8(1): 13-23.

Robichaud, D.A., Elner, R.W. and Bailey, R.F.J. 1991. Differential selection of crab *Chionoecetes opilio* and *Hyas* spp. as prey by sympatric cod *Gadus morhua* and thorny skate *Raja radiata*. Fish. Bull. 89(4): 669-680.

Robichaud, D.A., Lawton, P. and Strong, M.B. 2000. Exploratory fisheries for rock crab, *Cancer irroratus* and Jonah crab, *Cancer borealis*, in Canadian Lobster Fishing Areas 34, 35, 36 and 38. DFO Can. Sci. Advis. Sec. Res. Doc. 2000/051. 27 p.

Robinson, S.M.C., Bernier, S. and MacIntyre, A. 2001. The impact of scallop drags on sea urchin populations and benthos in the Bay of Fundy, Canada. Hydrobiologia 465: 103-114.

Rochette, R., Morissette, S. and Himmelman, J.H. 1995. A flexible response to a major predator provides the whelk *Buccinum undatum* L. with nutritional gains. J. Exp. Mar. Biol. Ecol. 185: 167-180.

Rochette, R., Tétreauly, F. and Himmelman, J.H. 2001. Aggregation of whelks, *Buccinum undatum*, near feeding predators: the role of reproductive requirements. Anim. Behav. 61: 31-41.

Roddick, D.L. and Kenchington, E. 1990. A review of the Banquereau Bank fishery for *Mactromeris polynyma* for the 1986 to 1989 period. CAFSAC Res. Doc. 90/14. 27 p.

Roddick, D., Kilada, R. and Mombourquette, K. 2007. Assessment of the Arctic surfcalam (*Mactromeris polynyma*) stock on Banquereau, Nova Scotia, 2004. CSAS Res. Doc. 2007/035. 39 p.

Roddick, D.L. and Lemon, D. 1992. Exploratory survey for small Arctic surfclams on the eastern Scotian Shelf. Can. Ind. Rep. Fish. Aquat. Sci. 215. 33 p.

Roddick, D. and Smith, S.J. 1999. Assessment of the Banquereau Bank Arctic Surfclam, 1999. DFO CSAS Res. Doc. 1999/69. 29 p.

Roegner, G.C. 2000. Transport of molluscan larvae through a shallow estuary. J. Plankton Res. 22(9): 1779-1800.

Roegner, G.C., Armstrong, D.A., Hickey, B.M. and Shanks, A.L. 2003. Ocean distribution of Dungeness crab megalopae and recruitment patterns to estuaries in southern Washington State. Estuaries 26(4B): 1058-1070.

Roff, J.C., Davidson, K.G., Pohle, G. and Dadswell, M.J. 1984a. A guide to the marine flora and fauna of the Bay of Fundy and Scotian Shelf: Larval Decapoda: Brachyura. Can. Tech. Rep. Fish. Aquat. Sci. 1322: iv + 57 p.

Roff, J.C., Fanning, L.P. and Stasko, A.B. 1984b. Larval crab (Decapoda: Brachyura) zoeas and megalopsa of the Scotian Shelf. Can. Tech. Rep. Fish. Aquat. Sci. 1264. 22 p.

Rogers-Bennett, L., Bennett, W.A., Fastenay, H.C. and Dewees, C.M. 1995. Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. Ecol. Appl. 5: 1171-1180.

Roller, R.A. and Stickle, W.B. 1985. Effects of salinity on larval tolerance and early developmental rates of four species of echinoderms. Can. J. Zool. 63: 1531-1538.

Roper, C.F.E., Sweeney, M.J. and Nauen, C.E. 1984. FAO Species Catalogue: Cephalopods of the World. FAO Fisheries Synopsis No. 125, Volume 3. 277 p.

Ropes, J.W. 1978. Biology and distribution of surfclams (Spisula solidissima) and ocean quahogs (*Arctica islandica*) off the northeast coast of the United States. Proc. Northeast Clam Industries: Management for the Future, April 27 and 28, 1978 Hyannis, Massachusetts. p. 47-66. Coop. Ext. Ser. Univ. Mass.-MIT Sea Grant Rept. SP 112.

Ropes, J.W., Serchuk, F.M. and Murawski, S.A. 1981. Studies of ocean quahogs off Shinnecock Inlet, Long Island. Coastal Oceanography and Climatology News Spring 3(3): 31-32.

Ross, K.A., Thorpe, J.P. and Brand, A.R. 2004. Biological control of fouling in suspended scallop cultivation. Aquaculture 229: 99-116.

Rossi, S., Gili, J.M. and Hughes, R.G. 2000. The effects of exposure to wave action on the distribution and morphology of the epiphytic hydrozoans *Clava multicornis* and *Dynamena pumila*. Sci. Mar. (Barc.) 64: 135-140.

Rountree, R.A. and Able, K.W. 1992a. Fauna of polyhaline subtidal marsh creeks in southern New Jersey: composition, abundance and biomass. Estuaries 15(2): 171-185.

Rountree, R.A. and Able, K.W. 1992b. Foraging habits, growth and temporal patterns of salt-marsh creek habitat use by young-of-year summer flounder in New Jersey. Trans. Amer. Fish. Soc. 121: 765-776.

Rountree, R.A. and Able, K.W. 1996. Seasonal abundance, growth and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary. Fish. Bull. 94: 522-534.

Rowe, S. 2001. Movement and harvesting mortality of American lobsters (*Homarus americanus*) tagged inside and outside no-take reserves in Bonavista Bay, Newfoundland. Can. J. Fish. Aquat. Sci. 58: 1336-1346.

Rowe, S., Jones, I.L., Chardine, J.W., Elliot, R.D. and Veitch, B.G. 2000. Recent changes in the winter diet of murres (*Uria* spp.) in coastal Newfoundland waters. Can. J. Zool. 78: 495-500.

Rowell, T.W. 1989. Underwater World: Squid. Communications Directorate, Department of Fisheries and Oceans, Ottawa, Ontario. 6 p.

Rowell, T.W. and Amaratunga, T. 1986. Distribution, abundance and preliminary estimates of production potential for the ocean quahog (*Arctica islandica*) and Stimpson's surfclam (*Spisula polynyma*) on the Scotian Shelf. CAFSAC Res. Doc. 86/56. 21 p.

Rowell, T.W., Chaisson, D.R. and McLane, J.T. 1990. Size and age of sexual maturity and annual gametogenic cycle in the ocean quahog, *Arctica islandica* (Linnaeus, 1767), from coastal water in Nova Scotia, Canada. J. Shellfish Res. 9(1): 195-203.

Ruiz, G.M., Hines, A.H. and Posey, M.H. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: an example from Chesapeake Bay. Mar. Ecol. Prog. Ser. 99: 1-16.

Russell, M.P., Ebert, T.A. and Petraitis, P.S. 1998. Field estimates of growth and mortality of the green sea urchin, *Strongylocentrotus droebachiensis*. Ophelia 48(2): 137-153.

Russell, M.P. and Meredith, R.W. 2000. Natural growth lines in echinoid ossicles are not reliable indicators of age: a test using *Stronglyocentrotus droebachiensis*. Invertebr. Biol. 119: 410-420.

Ryan, C.M. 2000. Effect of algal cell density, dietary composition, growth phase and macronutrient concentration on growth and survival of giant scallop *Placopecten magellanicus* (Gmelin, 1791) larvae and spat in a commercial hatchery. Thesis (M.Sc.), Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 98 p.

Ryland, J.S. 1959. Experiments on the selection of algal substrates by polyzoan larvae. J. Exp. Biol. 36: 613-631.

Ryland, J.S. 1962. The association between Polyzoa and algal substrata. J. Anim. Ecol. 31: 331-338.

Ryland, J.S. 2001. Convergent colonial organization and reproductive function in two bryozoan species epizoic on gastropod shells. J. Nat. Hist. 35: 1085-1101.

Ryland, J.S. and Hayward, P.J. 1991. Marine flora and fauna of the northeastern United States: erect bryozoa. NOAA Tech. Rep. NMFS 99. U.S. Department of Commerce. 48 p.

Ryland, J.S. and Porter, J.S. 2000. *Alcyonidium reticulum* sp. nov., a common intertidal bryozoan from south-west Britain. J. Mar. Biol. Assoc. U.K. 80: 563-564.

Saborowski, R., Salomon, M. and Buchholz, F. 2000. The physiological response of Northern krill (*Meganyctiphanes norvegica*) to temperature gradients in the Kattegat. Hydrobiologia 426: 157-160.

Sagasti, A., Schaffner, L.C. and Duffy, J.E. 2000. Epifaunal communities thrive in an estuary with hypoxic episodes. Estuaries 23(4): 474-487.

Saier, B. 2000. Age-dependent zonation of the periwinkle *Littorina littorea* (L.) in the Wadden Sea. Helgol. Mar. Res. 54: 224-229.

Saier, B. 2002. Subtidal and intertidal mussel beds (*Mytilus edulis* L.) in the Wadden Sea: diversity differences of associated epifauna. Helgol. Mar. Res. 56: 44-50.

Saier, B. and Chapman, A.S. 2004. Crusts of the alien bryozoan *Membranipora membranacea* can negatively impact spore output from native kelps (*Laminaria longicruris*). Bot. Mar. 47: 265-271.

Sainte-Marie, B. and Chabot, D. 2002. Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands. Fish. Bull. 100(1): 106-116.

Sainte-Marie, B. and Lafrance, M. 2002. Growth and survival of recently settled snow crab Chionoecetes opilio in relation to intra- and intercohort competition and cannibalism: a laboratory study. Mar. Ecol. Prog. Ser. 244: 191-203.

Sainte-Marie, B., Raymond, S. and Brêthes, J.-C. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. 52: 903-924.

Sameoto, D.D. 1980. Relationships between stomach contents and vertical migration in *Meganyctiphanes norvegica*, *Thysanoessa raschii* and *T. inermis* (*Crustacea Euphausiacea*). J. Plankton Res. 2(2): 129-143.

Sameoto, D. and Cochrane, N. 1996. Euphausiids on the eastern Continental Shelf. DFO Atl. Fish. Res. Doc. 96/119. 12 p.

Santos, M.B., Pierce, G., Hartmann, M.G., Smeenk, C., Addink, N., Kuiken, T., Reid, R.J., Patterson, I.A.P., Lordan, C., Rogan, E. and Mente, E. 2002. Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. J. Mar. Biol. Assoc. U.K. 82(3): 501-507.

Saunders, M. and Metaxas, A. 2007. Temperature explains settlement patterns of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 344: 95-106.

Sauve, S., Brousseau, P., Pellerin, J., Morin, Y., Senecal, L., Goudreau, P. and Fournier, M. 2002. Phagocytic activity of marine and freshwater bivalves: in vitro exposure of haemocytes to metals (Ag, Cd, Hg and Zn). Aquat. Toxicol. 58(3-4): 189-200.

Scaplen, R.P. 1970. Survey of shellfish (*Mytilus edulis* Linnaeus, The Blue Mussel) in Bonavista Bay and the potential mussel fishery. Report for the Newfoundland Fisheries Development Authority and the Industrial Development Branch, Canada Department of Fisheries and Forestry. 55. 9 p.

Scarrat, D.J. 1980. The food of lobsters. p. 66-91. *In* Pringle, J.D., Sharp, G.J. and Caddy, J.F. (eds.). Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can. Tech. Rep. Fish. Aquat. Sci. 954.

Scheibling, R.E., 1984. Echinoids, epizootics and ecological stability in the rocky subtidal off Nova Scotia, Canada. Helgoländer Meeresun. 37: 233-242.

Scheibling, R.E., Gagnon, P., 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Mar. Ecol. Prog. Ser. 325: 1-14.

Scheibling, R.E. and Hennigar, A.W. 1997. Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachiensis* in Nova Scotia: evidence for a link with large-scale meteorologic and oceanographic events. Mar. Ecol. Prog. Ser. 152: 155-165.

Scheibling, R.E., Henniger, A.W. and Balch, T. 1999. Destructive grazing, epiphytism and disease: the dynamics of sea urchin-kelp interactions in Nova Scotia. Can. J. Fish. Aquat. Sci. 56: 2300-2314.

Schneider, D. 1982. Escape response of an infaunal clam *Ensis directus* Conrad 1843, to a predatory snail, *Polinices duplicatus* Say 1822. Veliger 24(4): 371-376.

Schneider, G. 1993. Does *Aurelia aurita* really decimate zooplankton in Kiel Bight? ICES CM 1993/L:20. Biological Oceanography Committee. 23 p.

Schwaninger, H.R. 1999. Population structure of the widely dispersing marine bryozoan *Membranipora membranacea* (Cheilostomata): implications for population history, biogeography and taxonomy. Mar. Biol. 135: 411-423.

Scully, E.P. 1978. Utilization of surface foam as a food source by the hermit crab *Pagurus longicarpus* Say, 1817. Mar. Freshw. Behav. Phy. 5: 159-162.

Sebens, K. 1981. The allometry of feeding, energetics and body size in three sea anemone species. Biol. Bull. 161: 152-171.

Sebens, K.P. and Koehl, M.A.R. 1984. Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actinaria) in the New England subtidal. Mar. Biol. 81: 255-271.

Seed, R. 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores: II Growth and mortality. Oecologia 3: 317-350.

Seed, R. and O'Connor, R.J. 1981. Epifaunal associates of *Fucus serratus* at Dale, south-west Wales. Holarctic Ecol. 4: 1-11.

Sephton, T.W. 1987. The reproductive strategy of the Atlantic surfclam, *Spisula solidissima*, in Prince Edward Island, Canada. J. Shellfish Res. 6(2): 97-102.

Shanks, A.L. and del Carmen, K.A. 1997. Larval polychaetes are strongly associated with marine snow. Mar. Ecol. Prog. Ser. 154: 211-221.

Shick, J.M. and Hoffmann, R.J. 1980. Effects of the trophic and physical environments on asexual reproduction and body size in the sea anemone *Metridium senile*. *In* Tardent, P. and Tardent, R. (eds.). Developmental and cellular biology of coelentaerates. Amsterdam: Elsevier.

Short, F.T., Matso, K., Hoven, H.M., Whitten, J., Burdick, D.M. and Short, C.A. 2001. Lobster use of eelgrass habitat in the Piscataqua River on the New Hampshire/Maine border, U.S.A. Estuaries 24(2): 277-284.

Shumway, S.E., Bogdanowicz, C. and Dean, D. 1988. Oxygen consumption and feeding rates of the sabellid polychaete, *Myxicola infundibulum* (Renier). Comp. Biochem. Physiol. 90A(3): 425-428.

Shumway, S.E., Frank, D.M., Ewart, L.M. and Ward, J.E. 2003. Effect of yellow loess on clearance rate in seven species of benthic, filter-feeding invertebrates. Aquacult. Res. 34: 1391-1402.

Siddon, C.E. and Witman, J.D. 2003. Influence of chronic, low-level hydrodynamic forces on subtidal community structure. Mar. Ecol. Prog. Ser. 261: 99-110.

Siegel, V. 2000. Krill (*Euphausiacea*) life history and aspects of population dynamics. Can. J. Fish. Aquat. Sci. 57(Suppl. 3): 130-150.

Simard, Y., de Ladurantaye, R. and Therriault, J.-C. 1986b. Aggregation of euphausiids along a coastal shelf in an upwelling environment. Mar. Ecol. Prog. Ser. 32: 203-215.

Simard, Y., Lacroix, G. and Legendre, L. 1986a. Diel vertical migrations and nocturnal feeding of a dense coastal frill scattering layer (*Thysanoessa raschii* and *Meganyctiphanes norvegica)* in stratifed surface waters. Mar. Biol. 91: 93-105.

Simard, Y. and Lavoie, D. 1999. The rich krill aggregation of the Saguenay-St. Lawrence Marine Park: hydroacoustic and geostatistical biomass estimates, structure, variability and significance for whales. Can. J. Fish. Aquat. Sci. 56: 1182-1197.

Simard, Y., Lavoie, D. and Saucier, F.J. 2002. From plankton to whales: Oceanography of a traditional whale feeding ground and marine park in the St. Lawrence Estuary. ICES CM 2002/N:14. 12 p.

Simon, M.J., Kristensen, T.K., Tendal, O.S., Kinze, C.C. and Tougaard, S. 2003. *Gonatus fabricii* (Mollusca, Theuthida) as an important food source for sperm whales (*Physeter macrocephalus*) in the Northeast Atlantic. Sarsia 88(3): 244-246.

Singh, R., MacDonald, B.A., Lawton, P. and Thomas, M.L.H. 1998. Feeding response of the dendrochirote sea cucumber *Cucumaria frondosa* (Echinodermata: Holothuroidea) to changing food concentrations in the laboratory. Can. J. Zool. 76: 1842-1849.

Singh, R., MacDonald, B.A., Lawton, P. and Thomas, M.L.H. 2001. The reproductive biology of the dendrochirote sea cucumber Cucumaria frondosa (Echinodermata: Holothuroidea) using new quantitative methods. Invertebr. Reprod. Develop. 40(2-3): 125-141.

Singh, R., MacDonald, B.A., Thomas, M.L.H. and Lawton, P. 1999. Patterns of seasonal and tidal feeding activity in the dendrochirote sea cucumber *Cucumaria frondosa* (Echinodermata: Holothuroidea) in the Bay of Fundy, Canada. Mar. Ecol. Prog. Ser. 187: 133-145.

Sivertsen, K. 1997. Geographic and environmental factors affecting the distribution of kelp beds and barren grounds and changes in biota associated with kelp reduction at sites along the Norwegian coast. Can. J. Fish. Aquat. Sci. 54: 2872-2887.

Skilleter, G.A. 1994. Refuges from predation and the persistence of estuarine clam populations. Mar. Ecol. Prog. Ser. 109: 29-42.

Sloan, N.A. and Gunn, C.R. 1985. Fishing, processing and marketing of the jellyfish, *Aurelia aurita* (L.), from southern British Columbia. Can. Ind. Rep. Fish. Aquat. Sci. 157. 29 p.

Smith, B.C. and Wikfors, G.H. 1992. Phytoplankton pigments accumulated by the Arctic surfclam, *Mactromeris polynyma* (Stimpson, 1860). J. Shellfish Res. 11(2): 479-483.

Snelgrove, P.V.R., Grant, J. and Pilditch, C.A. 1999b. Habitat selection and adult-larvae interactions in settling larvae of softshell clam *Mya arenaria*. Mar. Ecol. Prog. Ser. 182: 149-159.

Snelgrove, P.V.R., Grassle, J.P. and Butman, C.A. 1998. Sediment choice by settling larvae of the bivalve, *Spisula solidissima* (Dillwyn), in flow and still water. J. Exp. Mar. Biol. Ecol. 231: 171-190.

Snelgrove, P.V.R., Grassle, J.P., Grassle, J.F., Petrecca, R.F. and Ma, H. 1999a. In situ habitat selection by settling larvae of marine soft-sediment invertebrates. Limnol. Oceanogr. 44(5): 1341-1347.

Snelgrove, P.V.R., Grassle, J.F., Grassle, J.P., Petrecca, R.F. and Stocks, K.I. 2001. The role of colonization in establishing patterns of community composition and diversity in shallow-water sedimentary communities. J. Mar. Res. 59(5): 813-830.

Sokolova, I.M. and Pörtner, H.O. 2001. Temperature effects on key metabolic enzymes in *Littorina saxatilis* and *L. obtusata* from different latitudes and shore levels. Mar. Biol. 139: 113-126.

Sommer, A.M. and Pörtner, H.O. 2002. Metabolic cold adaptation in the lugworm *Arenicola marina*: comparison of a North Sea and a White Sea population. Mar. Ecol. Prog. Ser. 240: 171-182.

Sommer, U. 2000. Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. Oecologia 122: 284-287.

Sornes, T.A. and Aksnes, D.L. 2004. Predation efficiency in visual and tactile zooplanktivores. Limnol. Oceanogr. 49(1): 69-75.

Squires, H.J. 1957. Squid, *Illex illecebrosus*, in the Newfoundland fishing area. J. Fish. Res. Board Can. 14: 693-728.

Squires, H.J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian eastern Arctic. Fish. Res. Board Can. Rep. (Biol.) 810: 212 p.

Squires, H.J. 1968. Relation of temperature to growth and self-propagation in *Pandalus borealis* from Newfoundland. FAO Fish. Rep. 57: 243-250.

Squires, H.J. 1990. Decapod crustacea of the Atlantic coast of Canada. Can. Bull. Fish. Aquat. Sci. 221: 532 p.

Squires, H.J. 1996. Larvae of the hermit crab, *Pagurus arcuatus*, from the plankton (Crustacea, Decapoda). J. Northwest Atl. Fish. Sci. 18: 43-56.

Squires, H.J., Ennis, G.P. and Dawe, G. 1997. Decapod larvae from a nearshore area of northeastern Newfoundland (Crustacea, Decapoda). Sci. Counc. Stud. NAFO 30: 75-87.

Squires, H.J., Ennis, G.P. and Dawe, G. 2000. On biology of the shrimp *Eualus pusiolus* (Krøyer, 1841) (Crustacea, Decapoda) at St. Chad's, Newfoundland. Sci. Counc. Stud. NAFO 33: 1-10.

Squires, H.J., Ennis, G.P. and Dawe, G. 2001. On biology of two sympatric species of hermit crab (Crustacea, Decapoda, Paguridae) at St. Chad's, Newfoundland. Sci. Counc. Stud. NAFO 34: 7-17.

Staaland, H. 1972. Respiration, salinity preference and ecology of the three marine prosobranchs *Buccinum undatum* (L.), *Neptunea antiqua* (L.) and *Neptunea despecta* (L.). Nor. J. Zool. 20: 35-50.

Stachowicz, J.J. and Lindquist, N. 1997. Chemical defence among hydroids on pelagic *Sargassum*: predator deterrence and absorption of solar UV radiation by secondary metabolites. Mar. Ecol. Prog. Ser. 155: 115-126.

Stanley, D.J. and James, N.P. 1971. Distribution of *Echinarachnius parma* (Lamarck) and associated fauna on Sable Island Bank, southeast Canada. Smithson. Contrib. Earth Sci. 6: 1-23.

Starr, M., Himmelman, J.H. and Therriault, J.-C. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. Science 247: 1071-1074.

Starr, M., Therriault, J.-C., Conan, G.Y., Comeau, M. and Robichaud, G. 1994. Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. J. Plankton Res. 16(9): 1137-1147.

Stehlik, L.L. 1993. Diets of the brachyuran crabs *Cancer irroratus*, *C. borealis* and *Ovalipes ocellatus* in the New York Bight. J. Crust. Biol. 13(4): 723-735.

Stehlik, L.L., MacKenzie, C.L., Jr. and Morse, W.W. 1991. Distribution and abundance of four brachyuran crabs on the northwest Atlantic Shelf. Fish. Bull. 89: 473-492.

Stehlik, L.L. and Meise, C.J. 2000. Diet of winter flounder in a New Jersey estuary: ontogenetic change and spatial variation. Estuaries 23(3): 381-391.

Steimle, F.W. 1989. Population dynamics, growth and production estimates for the sand dollar *Echinarachnius parma*. Fish. Bull. 88(1): 179-189.

Steingrímsson, S.A. and Thórarinsdóttir, G. 1995. Age structure, growth and size at sexual maturity in ocean quahog, *Arctica islandica* (Mollusca: Bivalvia), off NW-Iceland. ICES CM 1995/K:54. 17 p.

Stepanjants, S.D. 1998. *Obelia* (Cnidaria, Medusozoa, Hydrozoa): Phenomenon, aspects of investigations, perspectives for utilization. Oceanogr. Mar. Biol. Annu. Rev. 36: 179-215.

Stephen, S.J. 1982. A checklist/key to cephalopods of the Canadian Atlantic. Huntsman Marine Laboratory, St. Andrews, New Brunswick. 236 p.

Stephens, R.E. 1972. Studies on the development of the sea urchin *Strongylocentrotus droebachiensis* I. Ecology and normal development. Biol. Bull. 142(1): 132-144.

Stickney, A.P. 1964. Salinity, temperature and food requirements of softshell clam larvae in laboratory culture. Ecology 45(2): 283-291.

Stokesbury, K.D.E. and Himmelman, J.H. 1996. Experimental examination of movement of the giant scallop, *Placopecten magellanicus*. Mar. Biol. 124: 651-660.

Storm, L. and Pedersen, S.A. 2003. Development and drift of northern shrimp larvae (*Pandalus borealis*) at West Greenland. Mar. Biol. 143: 1083-1093.

Strasser, M. 1998. Mya arenaria — an ancient invader of the North Sea coast. Helgol. Mar. Res.. 52(3-4): 309-324.

Ström, R. 1977. Brooding patterns of bryozoans. *In* Woollacott, R.M. and Zimmer, R.L. (eds.) Biology of bryozoans. Academic Press, New York, NY.

Strömberg, J.-O., Spicer, J.I., Liljebladh, B. and Thomasson, M.A. 2002. Northern krill, *Meganyctiphanes norvegica*, come up to see the last eclipse of the millennium? J. Mar. Biol. Assoc. U.K. 82: 919-920.

Sullivan, B.K., Garcia, J.R. and Klein-MacPhee, G. 1994. Prey selection by the scyphomedusan predator *Aurelia aurita*. Mar. Biol. 121: 335-341.

Sullivan, B.K., Suchman, C.L. and Costello, J.H. 1997b. Mechanics of prey selection by ephyrae of the scyphomedusa *Aurelia aurita*. Mar. Biol. 130: 213-222.

Sullivan, B., Williams, J., Van Keuren, D., Lough, R.G. and Manning, J. 1997a. Abundance and distribution of planktonic hydroids with respect to larval fish and hydrographic features on Georges Bank. ICES CM 1997/T:02. 7 p.

Sullivan, C.M. 1948. Bivalve larvae of Malpeque Bay, PEI. Fish. Res. Board Can., 77. 36 p.

Sullivan, K. 2004. Byssal thread production and locomotion in *Mytilus trossolus* versus *Mytilus edulis* under varying salinity, temperature and feeding conditions. Paper submitted for Advanced Diploma in Aquaculture, Marine Institute, St. John's, Newfoundland and Labrador.

Summers, W.C. 1971. Age and growth of *Loligo pealeii*, a population study of the common Atlantic coast squid. Biol. Bull. Mar. Biol. Lab. (Woods Hole) 141: 189-201.

Suthers, I.M. and Frank, K.T. 1990. Zooplankton biomass gradient off south-western Nova Scotia: nearshore ctenophore predation or hydrographic separation? J. Plankton Res. 12(4): 831-850.

Svavarsson, J., Granmo, Å, Ekelund, R. and Szpunar, J. 2001. Occurrence and effects of organotins on adult common whelk (*Buccinum undatum*) (Mollusca, Gastropoda) in harbours and in a simulated dredging situation. Mar. Poll. Bull. 42(5): 370-376.

Swennen, C., Leopold, M.F. and Stock, M. 1985. Notes on growth and behaviour of the American razor clam *Ensis directus* in the Wadden Sea and the predation on it by birds. Helgoländer Meeresun. 39: 255-261.

Tallqvist, M.E. and Sundet, J.H. 2000. Annual growth of the cockle *Clinocardium ciliatum in* the Norwegian Arctic (Svalbard area). Hydrobiologia 440: 331-338.

Tanasichuk, R.W. 2002. Implications of interannual variability in euphausiid population biology for fish production along the south-west coast of Vancouver Island: a synthesis. Fish. Oceanogr. 11(1): 18-30.

Tarling, G.A. 2003. Sex-dependent diel vertical migration in northern krill *Meganyctiphanes norvegica* and its consequences for population dynamics. Mar. Ecol. Prog. Ser. 260: 173-188.

Tarling, G., Burrows, M., Matthews, J., Saborowski, R., Buchholz, F., Bedo, A. and Mayzaud, P. 2000. An optimization model of the diel vertical migration of northern krill (*Meganyctiphanes norvegica*) in the Clyde Sea and the Kattegat. Can. J. Fish. Aquat. Sci. 57(Suppl. 3): 38-50.

Tarling, G.A. and Cuzin-Roudy, J. 2003. Synchronization in the molting and spawning activity of northern krill (*Meganyctiphanes norvegica*) and its effect on recruitment. Limnol. Oceanogr. 48(5): 2020-2033.

Tarling, G.A., Cuzin-Roudy, J. and Buchholz, F. 1999. Vertical migration behaviour in the northern krill *Meganyctiphanes norvegica* is influenced by moult and reproductive processes. Mar. Ecol. Prog. Ser. 190: 253-262.

Tarnowski, M.L. 1981. Temporal distribution of surfclam larvae off southern New Jersey. Abstracts: Annual Meeting, August 2-6, National Shellfisheries Association, Williamsburg, Virginia. 108 p.

Tavares, M. and De Melo, G.A.S. 2004. Discovery of the first known benthic invasive species in the Southern Ocean: the North Atlantic spider crab *Hyas araneus* found in the Antarctic Peninsula. Antarct. Sci. 16(2): 129-131.

Taylor, D.M. 1996. Aspects of multiparous snow crab (*Chionoecetes opilio*) fecundity in insular Newfoundland waters. M.Sc. Thesis, Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland. 93 p.

Taylor, D.L. 2003. Size-dependent predation on post-settlement winter flounder *Pseudopleuronectes americanus* by sand shrimp *Crangon septemspinosa*. Mar. Ecol. Prog. Ser. 263: 197-215.

Taylor, D.L. and Collie, J.S. 2003a. Effect of temperature on the functional response and foraging behavior of the sand shrimp *Crangon septemspinosa* preying on juvenile winter flounder *Pseudopleuronectes americanus*. Mar. Ecol. Prog. Ser. 263: 217-234.

Taylor, D.L. and Collie, J.S. 2003b. A temperature- and size-dependent model of sand shrimp (*Crangon septemspinosa*) predation on juvenile winter flounder (*Pseudopleuronectes americanus*). Can. J. Fish. Aquat. Sci. 60: 1133-1148.

Taylor, D.M., Hooper, R.G. and Ennis, G.P. 1985. Biological aspects of the spring breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, Newfoundland (Canada). Fish. Bull. 83(4): 707-711.

Tegner, M.J. and Dayton, P.K. 2000. Ecosystem effects of fishing in kelp forest communities. ICES J. Mar. Sci. 57: 579-589.

Temkin, M.H. 1994. Gamete spawning and fertilization in the gymnolaemate bryozoan *Membranipora membranacea*. Biol. Bull. 187: 143-155.

Temkin, M.H. 1996. Comparative fertilization biology of gymnolaemate bryozoans. Mar. Biol. 127: 329-339.

Teo, S.L.-M. and Ryland, J.S. 1995. Potential antifouling mechanisms using toxic chemicals in some British ascidians. J. Exp. Mar. Biol. Ecol. 188: 49-62.

Therkildsen, N.O. and Petersen, C.W. 2006. A review of the emerging fishery for the sea cucumber *Cucumaria frondosa*: biology, policy and future prospects. Beche-de-mer Inf. Bull. 23: 16-25.

Thiel, M., Stearns, L.M. and Watling, L. 1998. Effects of green algal mats on bivalves in a New England mud flat. Helgoländer Meeresun. 52: 15-28.

Thomas, M.L.H. and Himmelman, J.H. 1988. Influence of predation on shell morphology of *Buccinum undatum* L. on Atlantic coast of Canada. J. Exp. Mar. Biol. Ecol. 115: 221-236.

Thompson, I., Jones, D.S. and Driebelbis, D. 1980. Annual internal growth banding and life history of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). Mar. Biol. 57: 25-34.

Thompson, J.C. 2002. The influence of hunger and olfactory cues on the feeding behavior of the waved whelk, *Buccinum undatum*, on the blue mussel, *Mytilus edulis*. Veliger 45(1): 55-57.

Thompson, R.J. 1979. Fecundity and reproductive effort in the blue mussel (*Mytilus edulis*) the sea urchin (*Strongylocentrotus droebachiensis*) and the snow crab (*Chionoecetes opilio*) from populations in Nova Scotia and Newfoundland. J. Fish. Res. Board Can. 36: 955-964.

Thórarinsdóttir, G.G. 1997. Distribution and abundance of juvenile ocean quahog (*Arctica islandica*) in Eyjafjördur North Iceland. ICES CM 1997/BB:17. Shellfish Committee. 9 p.

Thórarinsdóttir, G.G. and Einarsson, S.T. 1996. Distribution, abundance, population structure and meat yield of the ocean quahog, *Arctica islandica*, in Icelandic waters. J. Mar. Biol. Assoc. U.K. 76: 1107-1114.

Thórarinsdóttir, G.G. and Steingrímsson, S.A. 2000. Size and age at sexual maturity and sex ratio in ocean quahog, *Arctica islandica* (Linnaeus, 1767), off northwest Iceland. J. Shellfish Res. 19(2): 943-947.

Timofeev, S.F. 2000. Discovery of eggs and larvae of *Thysanoessa raschii* (M. Sars, 1846) (Euphausiacea) in the Laptev Sea: proof of euphausiids spawning on the shelf of the Arctic Ocean. Crustaceana 73(9): 1089-1094.

Timofeev, S.F. and Sklyar, V.V. 2002. Egg size in the euphausiid, *Thysanoessa raschii* (M. Sars, 1864) (Euphausiacea) in the Barents Sea. Crustaceana 74(11): 1201-1211.

Tkachenko, K.S. 2003. Distribution of the anthozoan *Metridium senile fibriatum* (Verril) on the rocky sublittoral of the Rimsky-Korsakov Islands, Sea of Japan. Russian J. Ecol. 34(4): 271-276.

Tkachenko, K.S. and Zhirmunsky, A.V. 2002. Distribution of sessile invertebrates in a rocky sublittoral community off Rimsky-Korsakov Islands (Sea of Japan). Mar. Ecol. 23(3): 253-267.

Torgersen, T. 2001. Visual predation by the euphausiid *Meganyctiphanes norvegica.* Mar. Ecol. Prog. Ser. 209: 295-299.

Toro, J.E., Thompson, R.J. and Innes, D.J. 2002. Reproductive isolation and reproductive output in two sympatric mussel species (*Mytilus edulis*, *M. trossulus*) and their hybrids from Newfoundland. Mar. Biol. 141: 897-909.

Toyokawa, M., Toda, T., Kikuchi, T., Miyake, H. and Hashimoto, J. 2003. Direct observations of a dense occurrence of *Bolinopsis infundibulum* (Ctenophora) near the seafloor under the Oyashio and notes on their feeding behavior. Deep Sea Res. (I Oceanogr. Res. Pap.) 50(6): 809-813.

Tremblay, M.J., Eagles, M.D. and Black, G.A.P. 1998. Movements of the lobster, *Homarus americanus*, off northern Cape Breton Island, with notes on lobster catchability. Can. Tech. Rep. Fish. Aquat. Sci. 2220. 32 p.

Tremblay, M.J. and Reeves, A. 2000. Rock crab off Eastern Nova Scotia: Stock status and evaluation of exploratory fishery. DFO Can. Sci. Advis. Sec. Res. Doc. 2000/023. 25 p.

Tremblay, M.J., A. Reeves and T. Worcester. 2001. Major features of the distribution and life history of some commercially fished benthic invertebrates in the Sydney Bight area. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/122. 30 p.

Tremblay, M.J. and Sinclair, M. 1990. Diel vertical migration of sea scallop larvae *Placopecten magellanicus* in a shallow embayment. Mar. Ecol. Prog. Ser. 67: 19-25.

Trites, R.W. 1983. Physical oceanographic features and processes relevant to *Illex illecebrosus* spawning in the western North Atlantic and subsequent larval distribution. Sci. Counc. Stud. NAFO 6: 39-55.

Trussel, G.C. 2002. Evidence of countergradient variation in the growth of an intertidal snail in response to water velocity. Mar. Ecol. Prog. Ser. 243: 123-131.

Tsipoura, N. and Burger, J. 1999. Shorebirds and surfclams: An unusual interaction. Waterbirds 22(1): 140-141.

Tupper, M. and Able, K.W. 2000. Movements and food habits of striped bass (*Morone saxatilis*) in Delaware Bay (U.S.A.) salt marshes: comparison of a restored and a reference marsh. Mar. Biol. 137: 1049-1058.

Ushakova, O.O. 2003. Combined effect of salinity and temperature on *Spirorbis spirorbis* L. and *Circeus spirillum* L. larvae from the White Sea. J. Exp. Mar. Biol. Ecol. 296(1): 23-33.

Ushakova, O.O. and Sarantchova, O.L. 2004. The influence of salinity on fertilization and larval development of *Nereis virens* (Polychaeta, Nereidae) from the White Sea. J. Exp. Mar. Biol. Ecol. 301(2): 129-139.

Vadas Sr., R.L., Beal, B., Dowling, T. and Fegley, J.C. 2000. Experimental field tests of natural algal diets on gonad index and quality in the green sea urchin, *Strongylocentrotus droebachiensis*: a case for rapid summer production in post-spawned animals. Aquaculture 182: 115-135.

Vahl, O. 1982. Long-term variations in recruitment of the Iceland scallop, *Chlamys islandica*, from northern Norway. Neth. J. Sea Res. 16: 80-87.

Van der Meer, J., Beukema, J.J. and Dekker, R. 2000. Population dynamics of two marine polychaetes: the relative role of density dependence, predation and winter conditions. ICES J. Mar. Sci. 57: 1488-1494.

Van der Meeren, G.I. 2000. Predation on hatchery-reared lobsters released in the wild. Can. J. Fish. Aquat. Sci. 57: 1794-1803.

Van Hoey, G., Degraer, S. and Vincx, M. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. Estuar. Coast. Shelf Sci. 59: 599-613.

Van Winkle, D.H., Longnecker, K. and Blackstone, N.W. 2000. The effects of hermit crabs on hydractiniid hydroids. Mar. Ecol. 21(1): 55-67.

Valentinsson, D. 2002. Reproductive cycle and maternal effects on offspring size and number in the neogastropod *Buccinum undatum* (L.). Mar. Biol. 140: 1139-1147.

Vecchione, M. 1981. Aspects of the early life of *Loligo pealeii* (Cephalopoda; Myopsida). J. Shellfish Res. 1(2): 171-180.

Vecchione, M. and Pohle, G. 2002. Midwater cephalopods in the western North Atlantic Ocean off Nova Scotia. Bull. Mar. Sci. 71(2): 883-892.

Vidal, E.A.G., DiMarco, F.P., Wormuth, J.H. and Lee, P.G. 2002. Optimizing rearing conditions of hatchling loliginid squid. Mar. Biol. 140: 117-127.

Vinogradov, V.I. and Noskov, A.S. 1979. Feeding of short-finned squid, *Illex illecebrosus* and long-finned squid, *Loligo pealeii*, off Nova Scotia and New England, 1974-75. ICNAF Selected Papers 5: 31-36.

Viscido, S.V. 1994. Seasonal and spatial variations in the marine epibenthic decapod community at Beach Haven Ridge, N.J. M.Sc. Thesis, Rutgers University, Camden, N.J., U.S.A.

Viscido, S.V., Stearns, D.E. and Able, K.W. 1997. Seasonal and spatial patterns of an epibenthic decapod crustacean assemblage in northwest Atlantic continental shelf waters. Estuar. Coast. Shelf Sci. 45: 377-392.

Vollen, T., Albert, O.T. and Nilssen, E.M. 2004. Diet composition and feeding behaviour of juvenile Greenland halibut (*Reinhardtius hippoglossoides*) in the Svalbard area. J. Sea Res. 51(3-4: 251-259.

Wada, S., Kitaoka, H. and Goshima, S. 2000. Reproduction of the hermit crab *Pagurus lanuginosus* and comparison of reproductive traits among sympatric species. J. Crust. Biol. 20(3): 474-478.

Waddell, B.J., and Perry, R.I. 2007. Survey results of green sea urchin (*Strongylocentrotus droebachiensis*) populations in Queen Charlotte Strait, British Columbia, October, 2006. Can. Tech. Rep. Fish. Aquat. Sci. 2742: vii + 47 p.

Wahl, M. 1985. *Metridium senile*: dispersion and small scale colonization by the combined strategy of locomotion and asexual reproduction (laceration). Mar. Ecol. Prog. Ser. 26: 271-277.

Wahl, M. and Hoppe, K. 2002. Interactions between substratum rugosity, colonization density and periwinkle grazing efficiency. Mar. Ecol. Prog. Ser. 239: 239-249.

Wahle, R.A. and R.S. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster (Homarus americanus Milne Edwards): a demographic bottleneck? Mar. Ecol. Prog. Ser. 69: 231-243.

Wahle, R.A. and R.S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. J. Exp. Mar. Biol. Ecol. 157: 91-114.

Walker, C.W. and Fineblit, J. 1982. Interactions between adult and embryonic tissues during brooding in *Axiognathus squamata* (Echinodermata. Ophiuroidea). Am. Zool. 22: 861.

Walker, C.W. and Lesser, M.P. 1998. Manipulation of food and photoperiod promotes out-of-season gametogenesis in the green sea urchin, *Strongylocentrotus droebachiensis*: implications for aquaculture. Mar. Biol. 132: 663-676.

Walker, R.L. 2001. Effects of stocking density on growth and survival of Atlantic surfclams in bottom cages versus mesh bags. J. Shellfish Res. 20(3): 1173-1176.

Walker, R.L. and O'Beirn, F.X. 1996. Embryonic and larval development of *Spisula solidissima similis* (Say, 1822) (Bivalvia: Mactridae). Veliger 39(1): 60-64.

Wang, Z., Thiébaut, E. and Dauvin, J.C. 1995. Spring abundance and distribution of the ctenophore *Pleurobrachia pileus* in the Seine estuary: advective transport and diel vertical migration. Mar. Biol. 124: 313-324.

Watanabe, T. and Ishii, H. 2001. *In situ* estimation of ephyrae liberated from polyps of *Aurelia aurita* using settling plates in Tokyo Bay, Japan. Hydrobiologia 451: 247-258.

Watson, D.C. and Norton, T.R. 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). J. Exp. Mar. Biol. Ecol. 88: 193-211.

Watson, D.C. and Norton, T.R. 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. J. Exp. Mar. Biol. Ecol. 112: 61-72.

Watson, G.J., Williams, M.E. and Bentley, M.G. 2000. Can synchronous spawning be predicted from environmental parameters? A case study of the lugworm *Arenicola marina.* Mar. Biol. 136: 1003-1017.

Watson, W.H. III, Vetrovs, A. and Howell, W.H. 1999. Lobster movements in an estuary. Mar. Biol. 134: 65-75.

Way, E. 2002. Preliminary studies on the northern sand dollar, *Echinarachnius parma* (Lamarck), off the coast of eastern Newfoundland. B.Sc. Hons. Diss., Memorial University of Newfoundland, St. John's, Newfoundland and Labrador. 55 p.

Wehrtmann, I.S. 1991. How important are starvation periods in early larval development for survival of *Crangon septemspinosa* larvae? Mar. Ecol. Prog. Ser. 73: 183-190.

Wehrtmann, I.S. 1994. Larval production of the caridean shrimp, *Crangon septemspinosa*, in waters adjacent to Chesapeake Bay in relation to oceanographic conditions. Estuaries 17(2): 509-518.

Wieczorek, S.K. and Hooper, R.G. 1995. Relationship between diet and food availability in the snow crab *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. J. Crust. Biol. 15(2): 236-247.

Weinberg, J.R. 1999. Age-structure, recruitment and adult mortality in populations of the Atlantic surfclam, *Spisula solidissima*, from 1978 to 1997. Mar. Biol. 134: 113-125.

Weinberg, J.R. and Helser, T.E. 1996. Growth of the Atlantic surfclam, *Spisula solidissima*, from Georges Bank to the Delmarva Peninsula, U.S.A. Mar. Biol. 126: 663-674.

Weissberger, E.J. 1998. The effects of predation on recruitment of the surfclam, *Spisula solidissima*. Ph.D. Thesis, Rutgers University, New Jersey, U.S.A.

Weissberger, E.J. and Grassle, J.P. 2003. Settlement, first-year growth and mortality of surfclams, *Spisula solidissima*. Estuar. Coast. Shelf Sci. 56: 669-684.

Welsh, B.L. 1970. Some aspects of the vertical migration and predatory behaviour of the sand shrimp, *Crangon septemspinosa*. M. Sc. Thesis, University of Maryland, College Park, Maryland. 66 p.

Wentworth, C. 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30: 377-392.

Westholt, R., Kestler, P., Sicken, O. and Westheide, W. 2001. Effects of long-term ultraviolet radiation: the white form of *Metridium senile* (Anthozoa: Actinaria) as a potential biological indicator for ultraviolet. Helgol. Mar. Res. 55: 87-93.

Whitman, K.L., McDermott, J.J. and Oehrlein, M.S. 2001. Laboratory studies on suspension feeding in the hermit crab *Pagurus longicarpus* (Decapoda: Anomura: Paguridae). J. Crust. Biol. 21(3): 582-592.

Whomersley, P. and G.B. Picken. 2003. Long-term dynamics of fouling communities found on offshore installations in the North Sea. J. Mar. Biol. Assoc. U.K. 83: 897-901.

Widersten, B. 1968. On the morphology and development of some cnidarian larvae. Zool. Bidr. Uppsala 37: 139-182.

Wildish, D.J., Akagi, H.M. and Hamilton, N. 2000. Effect of velocity on horse mussel initial feeding behaviour. Can. Tech. Rep. Fish. Aquat. Sci. 2325. 13 p.

Wildish, D., Akagi, H., Hatt, B., Hamilton, N., Brock, V., Dalum, M., Gjerulff, C., Henriksen, B., Hesselberg, M., Jensen, B., Johannesen, P., Kristensen, L., Mackenhauer, B., Madsen, T., Michelsen, L., Nielsen, K., Norgaard, H., Olesen, D., Pedersen, L., Rosenkrands, T., Søndergård, B. and Stottrup, L. 1998a. Population analysis of horse mussels of the inner Bay of Fundy based on estimated age, valve allometry and biomass. Can. Tech. Rep. Fish. Aquat. Sci. 2257. 23 p.

Wildish, D.J., Fader, G.B.J., Lawton, P. and MacDonald, A.J. 1998b. The acoustic detection and characteristics of sublittoral bivalve reefs in the Bay of Fundy. Cont. Shelf Res. 18: 105-113.

Wildish, D.J., Kristmanson, D.D., Akagi, H.M. and Zemlack, T. 2001. Inconclusive experiments to determine whether skimming flow influences mussel growth rates. Can. Manuscr. Rep. Fish. Aquat. Sci. 2581. 38 p.

Wildish, D.J., Kristmanson, D.D. and Peer, D. 1981. Effect of tidal currents on suspension-feeding benthos in the Bay of Fundy. ICES CM 1981/L:33. Biological Oceanography Committee. 7 p.

Wildish, D.J. and Peer, D. 1981. Tidal current speed and production of benthic macrofauna in the lower Bay of Fundy. Proceedings of the Symposium on the Dynamics of Turbid Coastal Environments. Can. J. Fish. Aquat. Sci. 40(1): 309-321.

Williams, A.B. 1984. Shrimps, lobsters and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC. 550 p.

Williams, D.D. 2003. The brackishwater hyporheic zone: invertebrate community structure across a novel ecotone. Hydrobiologia 510: 153-173.

Williams, J.D. and McDermott, J.J. 2004. Hermit crab biocoenoses: a worldwide review of the diversity and natural history of hermit crab associates. J. Exp. Mar. Biol. Ecol. 305(1): 1-128.

Wilson, W.H., Jr. and Ruff, R.E. 1988. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic) – Sandworm and bloodworm. Fish Wildl. Serv., U.S. Dep. Int. and Coastal Ecology Group Waterways Experiment Station, U.S. Army Corps of Eng. Biol.Rep. 82 (11.80). 23 p.

Winston, J.E. 1977. Feeding in marine bryozoans. p. 233-271. *In* Woollacott, R.M. and Zimmer, R.L. (eds.). Biology of Bryozoans. Academic Press, New York, NY.

Winston, J.E. and Key, M.M. 1999. *Alcyonidium albescens* (Ectoprocta: Ctenostomata) a new species from the mid-Atlantic coast of the United States. Bull. Mar. Sci. 64(3): 509-512.

Witbaard, R., Duineveld, G.C.A. and de Wilde, P.A.W.J. 1999. Geographical differences in growth rates of *Arctica islandica* (Mollusca: Bivalvia) from the North Sea and adjacent waters. J. Mar. Biol. Assoc. U.K. 79: 907-915.

Witbaard, R., Franken, R. and Visser, B. 1997. Growth of juvenile *Arctica islandica* under experimental conditions. Helgoländer Meeresun. 51: 417-431.

Witbaard, R., Jansma, E. and Klaassen, U.S. 2003. Copepods link quahog growth to climate. J. Sea Res. 50(1): 77-83.

Witman, J.D. 1985. Refuges, biological disturbance and rocky subtidal community structure in New England. Ecol. Monogr. 55(4): 421-445.

Witman, J.D. 1987. Subtidal coexistence: storms, grazing, mutualism and the zonation of kelps and mussels. Ecol. Monogr. 57(2): 167-187.

Witman, J.D., Genovese, S.J., Bruno, J.F., McLaughlin, J.W. and Pavlin, B.I. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. Ecol. Monogr. 73(3): 441-462.

Witting, D.A. and K.W. Able. 1995. Predation by sevenspine bay shrimp *Crangon septemspinosa* on winter flounder *Pleuronectes americanus* during settlement: laboratory observations. Mar. Ecol. Prog. Ser. 123: 23-31.

Wong, M.C. and Barbeau, M.A. 2003. Effects of substrate on interactions between juvenile sea scallops (*Placopecten magellanicus* Gmelin) and predatory sea stars (*Asterias vulgaris* Verrill) and rock crabs (*Cancer irroratus* Say). J. Exp. Mar. Biol. Ecol. 287(2): 155-178.

Wong, W.H. and Levinton, J.S. 2004. Culture of the blue mussel *Mytilus edulis* (Linnaeus, 1758) fed both phytoplankton and zooplankton: a microcosm experiment. Aquacult. Res. 35: 965-969.

Wood, J.B., Kenchington, E. and O'Dor, R.K. 1998. Reproduction and embryonic development time of *Bathypolypus arcticus*, a deep-sea octopod (Cephalopoda: Octopoda). Malacologia 39(1-2): 11-19.

Yancey, R.M. and Welch, W.R. 1968. The Atlantic coast surfclam – with a partial bibliography. U.S. Dep. Int., Fish Wildl. Serv., Circular 288. 14 p.

Yoshioka, P.M. 1982. Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. Ecology 63: 457-468.

Young-Lai, W.W. and Aiken, D.E. 1986. Biology and culture of the giant scallop, *Placopecten magellanicus*: a review. Can. Tech. Rep. Fish. Aquat. Sci. 1478. 21 p.

Youngbluth, M.J., Bailey, T.G., Davoll, P.J., Jacoby, C.A., Blades-Eckelbarger, P.I. and Griswold, C.A. 1989. Fecal pellet production and diel migratory behaviour by the euphausiid *Meganyctiphanes norvegica* effect benthic-pelagic coupling. Deep Sea Res. (I Oceanogr. Res. Pap.) 36(10): 1491-1501.

Yund, P.O. and Meidel, S.K. 2003. Sea urchin spawning in benthic boundary layers: Are eggs fertilized before advecting away from the females? Limnol. Oceanogr. 48(2): 795-801.

Zettler, M.L., Bonsch, R. and Gosselck, F. 2001. Distribution, abundance and some population characteristics of the ocean quahog, *Arctica islandica* (Linnaeus, 1767), in the Mecklenburg Bight (Baltic Sea). J. Shellfish Res. 20(1): 161-169.

Zimmer, R.L. and Woollacott, R.M. 1977. Structure and classification of gymnolaemate larvae. p. 57-89. *In* Woollacott, R.M. and Zimmer, R.L. (eds.). Biology of bryozoans. Academic Press, New York, NY.

Zolotarev, P. 2002. Population density and size structure of sea stars on beds of Iceland scallop, *Chlamys islandica*, in the southeastern Barents Sea. Sarsia 87: 91-96.

APPENDIX A – GLOSSARY OF TERMS

Aboral - opposite to or away from the mouth.

Adult - life stage of fish where they have reached sexual maturity and are able to reproduce, but are not in spawning condition.

Aggregation - group of individuals of the same species gathered in the same place, but not socially organized or engaged in cooperative behaviour.

Agonistic Behaviour - aggressive or defensive social interaction.

Algae - simple rootless plants that grow in bodies of water, such as estuaries at rates in relative proportion to the amount of nutrients (e.g. nitrogen and phosphorus) available.

Algal Canopy - formed by the largest algal species, these are floating blades which extend meters above the seafloor or to the ocean surface. It forms a system of microenvironments with a sunny canopy region, a partially shaded middle and darkened seafloor.

Algal Epiphytic - to live on algae which provide mechanical support but no nutrients.

Amphipods - small crustaceans of the order Amphipoda, which are shrimp-like in form and have a laterally compressed body with no carapace (e.g., gammarids, beach fleas).

Anemone - flowerlike marine coelenterates of the class Anthozoa, having a flexible cylindrical body and tentacles surrounding a central mouth.

Annelid - a class of worms characterized by an elongated, cylindrical, segmented body (e.g., earthworms, leeches).

Anterior - located toward the front.

Anthozoans - a class of marine organisms, which have radial segments and grow singly or in colonies (e.g., corals and sea anemones).

Autotomy - the spontaneous casting off of a limb or other body part, such as the claw of a lobster, especially when the organism is injured or under attack.

Benthic - relating to the bottom of the sea or to the organisms that live there.

Benthic Organisms - individuals, most often invertebrates, that live on the bottom of the ocean for at least part of their life cycle, are typically immobile or of limited motility and are dependent upon the decomposition cycle for most, if not all, of their basic food supply.

Benthos - see Benthic Organisms.

Berried - bearing eggs.

Biota - all plant and animal life of a particular region.

Bivalve - a class of molluscs having a soft body with plate-like gills enclosed within two shells hinged together (e.g., clams, mussels).

Boulder Barricade - an accumulation of large boulders that is visible along a coast between low and half tide.

Brackish - water that has more salinity than freshwater, but not as much as seawater; usually results from mixing of seawater with freshwater, as in estuaries.

Bursa(e) - sac or sac-like body cavity(ies).

Byssal (or Byssus) Threads - thin, hair-like filaments secreted by some molluscs, such as mussels, that are used for attachment to substrates.

Cannibalistic - to feed on others of ones own kind.

Carapace - a chitinous case or shield covering the back or part of the back of species like crab, shrimp and other crustaceans.

Carnivore - animals that eat meat.

Carrion Feeders - animals that feed partly or wholly on the bodies of dead animals.

Cephalopod - class of marine molluscs which have a large head, large eyes, prehensile tentacles, and, in most species, an ink sac containing a dark fluid used for protection or defense (e.g., octopus, squid, cuttlefish or nautilus).

Chaetognath - a phylum of predatory marine worms (arrow worms) characterized by a transparent dart-shaped cuticle.

Chitons - molluscs in the class *Polyplacophora*, distinguished by their characteristic shells, which consist of eight overlapping plates.

Circumpolar - located or found in one of the Polar Regions.

Cladocerans - small crustaceans belonging to the orders, Anomopoda, Ctenopoda, Onychopoda or Haplopoda; commonly called water fleas.

Clone - an identical genetic copy.

Clutch - a group of eggs hatched together.

Cnidarians - animals which undergo alternation of generations, medusae (floating) and polyp (sessile), and which use stinging cells to capture prey (formerly called Coelenterata).

Coelenterates - a group of primitive aquatic animals that includes jellyfish, corals and sea anemones.

Comb Jelly - see Ctenophores.

Commensal - a relationship in which one organism derives food or other benefits from another organism without hurting or helping it.

Congener - organisms within the same genus.

Conspecific - belonging to the same species.

Copepods - tiny herbivorous crustaceans.

Coralline Algae - species of algae which secrete calcareous material during the process of growing over rock surfaces.

Crustaceans - invertebrates characterized by a hard outer shell and jointed appendages and bodies; they usually live in water and breathe through gills (e.g., barnacles, lobster, shrimp).

Cryptic - applied to fish that live amongst sheltering and concealing cover, or that have protective coloration.

Ctenophores - various marine animals of the phylum Ctenophora, having transparent, gelatinous bodies bearing eight rows of comb-like cilia used for swimming.

Decapod - a crustacean of the order Decapoda characteristically having five pairs of legs (e.g., crab, lobster, crayfish or shrimp).

Demersal - living on or near the bottom of the ocean.

Deposit Feeders - benthic organisms that feed on the film of non-living organic detritus settled on the ocean floor (e.g., sea cucumbers, brittle stars).

Depth - vertical distance from the ocean bottom to the water surface.

Detritus - accumulated organic debris from dead organisms, which is often an important source of nutrients in a food web.

Diel - refers to a 24-hour period.

Dioecious - possessing separate sexes, having both male and female individuals within a species.

Diurnal - a term used to describe fish that are primarily active during the day.

Dorsal - pertaining to the back.

Down Slope - movement toward the lower intertidal or shallow subtidal zone.

Ecdysis (or molting) - the shedding of an outer integument or layer of skin/shell, common in crustaceans.

Echinoderm - radially symmetrical marine invertebrates of the phylum Echinodermata, which having an internal calcareous skeleton and are often covered with spines (e.g., starfish, sea urchins, sea lilies and sea cucumbers).

Egg Mop - a communal site on the ocean floor where squid eggs are laid.

Endobenthic - to live within the sediment of the sea floor.

Epibenthos - animals living on or immediately above the seafloor.

Epibiont - an organism that lives on the surface of another living organism.

Epifaunal - living on the surface of a substrate, such as the sea floor, rocks, marine vegetation, pilings, etc.

Epiphytic - a mode of existence whereby an animal/plant grows on another animal/plant upon which it depends for mechanical support, but not for nutrients.

Estuarine - living in the lower part of a river or estuary where marine and freshwaters meet and mix.

Estuary - a semi-enclosed body of water that has a free connection with the open ocean, but is diluted by freshwater input (transitional environments between fresh and salt water). It has a wide salinity range (0.5 to 18 ppt) and although estuaries are influenced by oceanic processes such as waves, currents and tides, they tend to be sheltered, experience lower energy regimes and are much more influenced by terrestrial inputs (e.g., freshwater and sediments from rivers) than marine waters.

Euphausiids - a collection of small, shrimp-like marine crustaceans of the order Euphausiacea (e.g., krill).

Eurybathic - capable of occupying a wide range of depths.

Euryhaline - capable of tolerating a wide range of salinities.

Eurythermal - capable of tolerating a wide range of temperatures.

Excurrent - current running or flowing in an outward direction.

Fauna - animals.

Fecundity - the potential reproductive capacity of an individual or species; in a stricter sense, the number of eggs produced per female during a reproductive cycle.

Filter Feeders - organisms that feed on smaller organisms within the water by using a straining system, such as gill rakers, to hold the food while they expel the water (e.g., barnacle).

Fish Habitat - spawning grounds and nursery, rearing, food supply, overwintering and migration areas on which fish depend either directly or indirectly in order to carry out their life processes.

Gametes - eggs or sperm.

Gametogenesis - production of gametes (eggs and sperm).

Gammaridian - laterally compressed crustaceans which commonly inhabitat shallow brackish waters and usually constitute a major component of near-shore macrofaunal communities.

Gastropods - molluscs which generally construct a spiral shell and move by means of a broad foot (e.g., snails, abalones, sea slugs).

Gastrozooids - within a hydroid colony these are the feeding zooids, which typically bear tentacles and a mouth.

Geotaxis - oriented movement of a motile organism toward or away from a gravitational force.

Gonophore - structure bearing or consisting of a reproductive organ or part, such as a reproductive polyp or bud in a hydroid colony.

Gregarious - occurring together in groups.

Halocline - depth zone within which salinity changes rapidly.

Heat Coma - a reversible condition characterized by the loss of nervous integration and is manifested by cessation of locomotion, ventral curling of the foot and the inability to remain attached to the substrate.

Herbivore - animal that eats plants.

Hermaphrodite - organisms having both male and female reproductive organs either at the same time (synchronous hermaphrodite) or at different times (successive hermaphrodite) during the life cycle.

Holoplanktonic - to be planktonic for an organism's entire life cycle.

Hydranth - see Gastrozooid.

Hydrocaulus - a hydrozoan stalk (trunk and branches) from which zooids arise.

Hydroids - a colony of hydrozoan polyps that are usually polymorphic (comprising more than one kind of polyp or zooid).

Hydrorhiza - the rootstock or decumbent stem by which a hydroid is attached to other objects.

Ichthyoplankton - eggs and larvae of fish drifting in the water column.

Immobile - to remain motionless in one place.

Imposex - a descriptive term applied to some molluscs which, under the toxic effects of pollutants, develop sex organs that are in contrast to their actual sex.

Infauna - living in the substrate, especially in a soft sea bottom.

Intertidal - the area of shore located between high and low tides; which are alternately exposed and covered by tidal waters.

Invertebrates - collective term used for all animals that lack a vertebral column or backbone.

Juvenile - older than one year of age, which are similar in appearance to adults, but smaller and not sexually mature.

Kleptoparasite - an animal that takes prey from another that has caught, killed, or stored it.

Krill - a shrimp-like marine invertebrate zooplankton, also know as euphausiids.

Laminarians - pertaining to seaweeds of the genus Laminaria.

Larva - a discrete stage in many species, beginning with zygote formation and ending with metamorphosis.

Larvaceans - a class of small free-swimming tunicates.

Lecithotrophic - to live off yolk supplied via the egg.

Life Stage - an extended period during the life cycle of an organism that is characterized by little or no change in development (e.g., egg, larval, YOY, juvenile, adult, etc.).

Macroalgae - a biological term used to describe larger forms of algae, such as seaweeds, which are easily visible with the naked eye.

Macrophyte - individual alga which are large enough to be seen easily with the unaided eye.

Marine - aquatic environment characterized by high salinity (18 to 35 ppt) and directly affected by oceanic processes such as waves, currents and tides.

Marine Snow - macroscopic aggregations of detritus and microbes that provide a structured benthic-like habitat in the water column.

Medusa - one of the alternate generations of cnidarians; it is the bell-shaped form of various species of jellyfish.

Megalopa Stage - the last larval stage before metamorphosis in decopods; first post-larval stage.

Meroplankton - the portion of the plankton that spend only a part of their life cycles as drifters near the surface; it is typically the larval stage of marine animals.

Metamorphosis - a major structural change of body shape, such as the change from a larval form to a juvenile or adult form.

Molluscs - soft, unsegmented animals of the phylum Mollusca which usually secrete a calcareous shell; includes bivalves (mussels, oysters), cephalopods (squid, octopus) and gastropods (abalone, snails).

Morphometric - relative to measurements of the shape of an individual; body proportions.

Multiparous - to produce a brood two or more times.

Nauplii - the free-swimming first stages of the larva of certain crustaceans, having unsegmented bodies with three pairs of appendages and a single median eye.

Necrophagous - to scavenge on dead animal tissue.

Nekton - any marine animal with locomotive ability sufficient to override the drift of currents.

Nemertean - proboscis worms belonging to the phylum Nemertea, which are soft, unsegmented and able to stretch and contract.

Neustonic - to float on, or drift immediately underneath, the water surface.

Nocturnal - animal behavior characterized by being active during the night and sleeping/sheltering during the day.

Omnivore - animal able to feed on either plants or animals.

Ophiuroids - a large group (over 1600 species) of echinoderms that includes the brittle stars and basket stars.

Oral Disc - the top disc-like structure where the mouth is centrally located and tentacles are present around the outer ring.

Ovigerous - bearing eggs.

Paralarvae - immediate post-hatching form of cephalopod young that swim to the surface. When the paralarvae get too large to stay in the plankton layer, they descend to the bottom for the remainder of their lives.

Passive Tidal Advection - the horizontal movement of water as in an ocean current, that is usually related to temperature differences of water masses.

Pediveligers - a transitional, swimming-crawling larval stage (possessing a foot) that settles to the bottom.

Pelagic - refers to open ocean waters, either middle or surface water levels, which are not directly influenced by the shore or bottom.

Phototactic - the movement of an organism or a cell toward or away from a source of light.

Phytoplankton - small or microscopic plant life that floats in the open ocean (i.e., they cannot move independently of water currents).

Piscivorous - fish-eating.

Plankton - passively floating or only weakly swimming, small marine plants (phytoplankton) and animals (zooplankton), which drift in the ocean along with the water currents.

Planktotrophic - to feed on plankton.

Planula - the planktonic larval form produced by scleractinian corals and coelenterates.

Pleopods - one of the sets of paired abdominal appendages present on some aquatic crustaceans. The primary function is the carrying of eggs, however, they are usually adapted for swimming.

Polychaete - segmented worms of the phylum Annelida, which are characterized by fleshy paired appendages tipped with bristles or setae on each body segment (e.g., lugworm).

Polyp - the sessile generation of cnidarians, which has a hollow cylindrical body closed and attached at one end and opening at the other with a mouth surrounded by tentacles armed with nematocysts.

Population - a group of individuals of one species, found within a prescribed area and usually somewhat isolated from other groups of the same species.

ppt - parts per thousand (used as a measurement of salinity).

Predacious - to feed on live prey.

Primiparous - to produce a brood for the first time, or to have only one brood.

Proboscis - the slender, tubular feeding and sucking organ of certain invertebrates.

Protandric - having male sexual organs while young and female organs later in life.

Protozoans - minute single-celled animals.

Pseudofaeces - filtered material voided before ingestion occurs; common in many bivalve molluscs.

Pteropod - free-swimming form of gastropod snail, in which the anterior lobes of the foot are modified into broad flap-like wings for swimming.

Pulsed Breeding - increases in breeding activity/success in relation to various favourable conditions such as food availability, climate, predator density, etc.

Pycnocline - a layer across which there is a rapid change in water density with depth.

Raptorial - adapted for seizing prey.

Recruitment - the number of individuals surviving some arbitrary period of time after settlement.

Roe - eggs.

Rotifer - minute multicellular aquatic organisms of the phylum Rotifera, which have a wheel like ring of cilia at their anterior end.

Salinity - a measure of the salt concentration of water, usually measured in parts per thousand (ppt); higher salinity means more dissolved salts.

Scattering Layer - a concerntrated layer of organisms in the ocean that reflects and scatters sound waves.

Scavenger - an animal that consumes dead organic matter.

Schooling - behavioral grouping together of fish, which usually move together as a group.

Sea Urchin Barrens - habitat devoid of kelp beds due to excessive herbivory, primarily through grazing by echinoids.

Sedentary - a lifestyle characterized by little or no movement.

Sediment - matter that settles and accumulates on the bottom of a body of water.

Semelparous - used to describe an organism that reproduces just once during its lifetime and then dies.

Sessile - permanently attached, not free moving.

Seston - particulate matter suspended in seawater.

Settlement - permanent movement of individuals from the water column to the benthos (i.e., the time when an individual takes up permanent residence in the demersal habitat).

Siphons - tubular organs that take in and expel water.

Spat - the spawn of a bivalve mollusc.

Spawning - reproductive life stage of fish characterized by females and males depositing eggs and sperm into the water simultaneously or in succession.

Species - a group of closely related organisms which are capable of inter-breeding, and which are reproductively isolated from other groups of organisms; the basic unit of biological classification.

Statoliths - a mineralized (calcium or magnesium salt crystals) mass located within a sac-like structure (statocyst) present in some aquatic invertebrates. Innervated sensory hairs within the statocyst interact with the inertia of the statolith to provide feedback to the animal with respect to change in direction and balance.

Substrate - the materials which the ocean bottom is comprised of including bedrock, boulder, rubble, cobble, gravel, silt, sand, mud and detritus.

Subtidal Zone - the shallow water zone from the extreme low tide level to a depth of approximately 200 m. Although it is influenced by tides, it is never completely drained or exposed at low tide.

Suspension Feeders - organisms that feed by filtering food out of the water (e.g., copepods).

Tenacity - holding fast.

Test - a shell made of fused plates.

Thermocline - depth zone within which temperature changes maximally.

Truncated - the condition of being square or broad at the end, lacking an apex.

Veliger Larvae - first larval stage with a bivalve shell.

Ventral - relating to the front or lower surface of an animal.

Viviparous - giving birth to living offspring that develop within the mother's body.

Voracious - consuming or eager to consume great amounts of food.

Year Class - a group of fish that were spawned in the same year. By convention, the 'birth date' is set to January 1 and a fish must experience a summer before turning 1. For example, a fish that was spawned in February-April 1997 are all part of the 1997 year class. They would be considered age 0 in 1997, age 1 in 1998, etc. A fish spawned in October 1997 would have its birth date set to the following January 1 and would be considered age 0 in 1998, age 1 in 1999, etc.

Young-of-the-Year (YOY) - fish under one year of age.

Zoea - a larval form of crabs and other decapod crustaceans characterized by one or more spines on the carapace and rudimentary limbs on the abdomen and thorax.

Zooplankton - a broad categorization spanning a range of drifting/swimming organism sizes that include both small protozoans and large metazoans. It includes holoplanktonic organisms whose complete life cycle lies within the plankton, and meroplanktonic organisms that spend part of their life cycle in the plankton before graduating to either the nekton or sessile, benthic existence.